Vol. LIII No. 1

THE BOTANICAL GAZETTE

January 1912

Editor: JOHN M. COULTER

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The University of Chicago Press
CHICAGO, ILLINOIS

Agents
THE CAMBRIDGE UNIVERSITY PRESS, *London and Edinburgh*
WILLIAM WESLEY & SON, *London*
TH. STAUFFER, *Leipzig*
THE MARUZEN-KABUSHIKI-KAISHA, *Tokyo, Osaka, Kyoto*

The Botanical Gazette

A Monthly Journal Embracing all Departments of Botanical Science

Edited by JOHN M. COULTER, with the assistance of other members of the botanical staff of the University of Chicago.

Issued January 17, 1912

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VOLUME LIII NUMBER 1

THE

BOTANICAL GAZETTE

JANUARY 1912

MORPHOLOGY OF CERATOZAMIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 153

CHARLES J. CHAMBERLAIN

(WITH PLATE I AND SEVEN FIGURES)

Southern Mexico, with its three genera of cycads (*Dioon*, *Ceratozamia*, and *Zamia*), is the principal cycad region of the western hemisphere. Two of these genera, *Dioon* and *Ceratozamia*, may be confined to Mexico. Occasional reports indicate a wider distribution, but both genera are so commonly cultivated in parks, both in Mexico and farther south, that descriptions, even when supported by specimens, would need the addition of observation in the field before habitats could be established. The first two descriptions of *Dioon spinulosum*, by DYER (1) and by EICHLER (2), were based upon cultivated specimens, and in the localities cited, Progreso and Cordoba, the species does not occur except in cultivation.

Ceratozamia has been reported beyond Mexico, but whether from observation in the field or from cultivated specimens, is uncertain. It grows wild at Chavarrillo, where it is associated with *Dioon edule*, but the plants are only seedlings with 2 or 3 leaves, except on Monte Oscuro, where there are some specimens large enough to bear cones. Between Jalapa and the extinct crater of Naolinco is a beautiful valley, and on the Jalapa side of the mountains which rise from this valley, large fruiting plants of *Ceratozamia* are abundant, but are limited to a rather narrow vertical

distribution, the altitude of which was not determined. Most of my material came from this region, largely from the hacienda of Señor LUIS CARAZA.

It is a pleasure to acknowledge my indebtedness to Governor TEODORO A. DEHESA and Mr. ALEXANDER M. GAW. During my first trip to Mexico in 1904, I failed to find any *Ceratozamia*, except a few seedlings at Chavarrillo, but after I had returned to Chicago, Governor DEHESA stationed an officer near cultivated plants in the park at Jalapa, and the officer questioned country people until he found one who knew where the plant grew wild. The region was the mountainous slope of the valley just referred to. After that, cones were easily secured, and for six years Mr. GAW has sent cones at all seasons, until the series is very complete. Besides, I have been able to visit the valley myself, first in September 1906, and later in March 1908. On the latter trip, and again in September 1910, I found *Ceratozamia* in the mountains across the Papaloapan River at Tuxtepec, but the plants were rather small and bore no cones.

The plants in the valley, near Jalapa, I identified as *Ceratozamia mexicana*. There is considerable variation, aside from that which the leaves of cycads present at various stages in the growth of the plant, the variation appearing even in the cones, which show less variation than the vegetative structures.

In habitat *Ceratozamia* differs decidedly from *Dioon edule*, which grows in the open, exposed to blazing sunlight, while *Ceratozamia* is found in densely shaded places. The difference in light will be appreciated from the fact that a photographic plate which would be well exposed for *Dioon* in one-fifth of a second would require three minutes exposure for *Ceratozamia*. The *Ceratozamia* associated with *Dioon* at Chavarrillo always appeared stunted, with one, two, or three leaves, except on Monte Oscuro, where it is shaded by a dense growth of shrubs. Although *Ceratozamia* is not found in wet situations, it is associated with a luxuriant vegetation, while *Dioon edule* and the plants associated with it are xerophytic. The habitat of *Ceratozamia* resembles that of *Dioon spinulosum*, but the latter plant does not occur in the Jalapa region. In the Tuxtepex region *Ceratozamia* appears before the *Dioon* locality is reached, but I did not find the two growing together.

The trunk and leaves

The trunk of *Ceratozamia mexicana* seldom reaches 2 meters in length. It is rather slender, has an armor of persistent leaf bases,

FIG. 1.—*Ceratozamia mexicana* growing on a steep mountain side opposite Naolinco, near Jalapa.

and is often curved or prostrate. This habit is doubtless due to the fact that so many plants grow on steep slopes (fig. 1), for the apex

is always vertical. As in *Dioon*, the foliage display consists of two crowns, the latest fresh and bright green, while the previous one has a dull green color, or may appear pale or gray on account of the numerous small lichens which almost invariably incrust the leaves of the second crown. Few plants have more than 10 leaves in a crown, so that the foliage display of a large plant consists of about 20 leaves. On the larger plants the leaves are 1.5–2 meters in length and have 40–50 leaflets on each side, the leaflets measuring about 50 cm. in length and 2 cm. in width. The variation in the leaves of plants of different ages is readily seen from the fact that the first leaf of a seedling usually has 4 leaflets, sometimes only 2, and that these early leaves are shorter, thinner, and narrower than the leaves of old plants. Differences may also appear in the margins of the leaflets and in the spines on the lower part of the petiole, so that identifications based upon the leaf alone must be regarded with some suspicion.

A section of the adult stem shows that it is strictly monoxylic, with a very narrow zone of wood showing no growth rings (**3**).

The strobili

Strobili are not abundant, and occasionally Mr. GAW had difficulty in securing them. When very young, the ovulate and staminate strobili have the same general appearance, but even then they may be distinguished superficially by the much larger number of sporophylls on the staminate strobili, and by the fact that the staminate strobilus is somewhat conical, while the ovulate is cylindrical. At maturity the staminate strobilus is quite pointed, while the ovulate is very evenly cylindrical and is much larger.

THE STAMINATE STROBILUS

The staminate strobilus reaches its full size and sheds its pollen about the middle of March. The largest staminate strobili are about 20 cm. in length, but the average length is not more than 15 cm. A typical staminate strobilus is shown in fig. 2. The sporophylls are somewhat wedge-shaped, distinctly stalked, and are tipped by the two horny spines which give the name to the

genus. The sporangia are crowded over the entire abaxial surface of the sporophyll, with only a slight indication of any division into two groups by a sterile line through the center (fig. 3). The sori consist of three or four sporangia, with some two's and occasionally a single sporangium, the single sporangium being found more frequently at the top and bottom of the strobilus. The soral character is not always evident in a surface view, but is rather distinct after the pollen has been shed (fig. 3, *c*), and is easily seen by removing the sporangia or by examining sections (figs. 3, 4). Dehiscence begins in the peripheral sporangia of the sporophyll and progresses toward the axis of the cone, as shown in fig. 3, *b*. As in *Dioon edule*, the wall of the sporangium is thin at the sides and thicker at the top, with a thick-walled outer layer of cells and thin-walled cells between this and the sporogenous tissue. The dehiscence is marked by two rows of thin-walled cells which contrast sharply with the thick-walled cells of the rest of the outer layer. The cells of the outer layer are elongated parallel to the dehiscence, so that in a section at a right angle to the dehiscence they are almost square in outline (fig. 5), while in a sec-

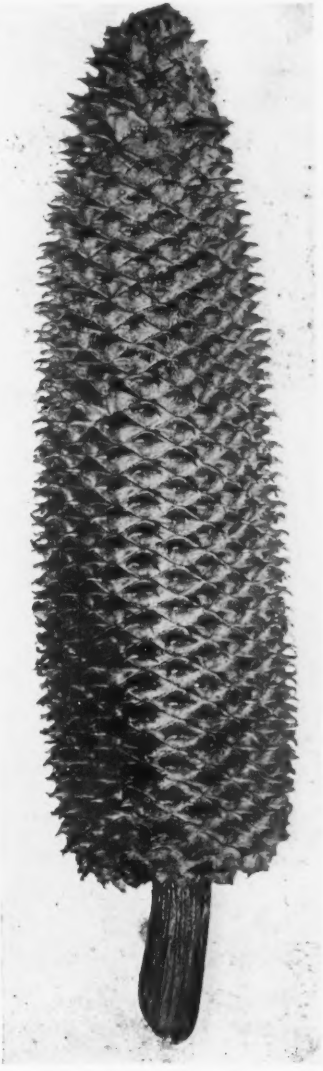


FIG. 2.—Staminate strobilus; $\times\frac{2}{3}$.

tion parallel to the dehiscence the length is several times as great as the breadth.

THE OVULATE STROBILUS

The ovulate strobilus is cylindrical in outline, and when mature is green and smooth. There is such variation in the size and general appearance of the strobilus that if one considered only the extremes he could easily describe new species. What may be regarded as extremes in the appearance of large cones is represented in figs. 6 and 7. The largest cone noted in several year's collections was 33.5 cm. in length and 11 cm. in diameter, and the smallest measured 21×8.5 cm. The average size is about 26.3×9.7 cm.

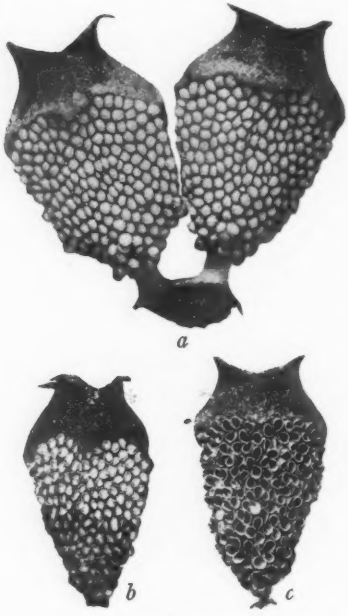


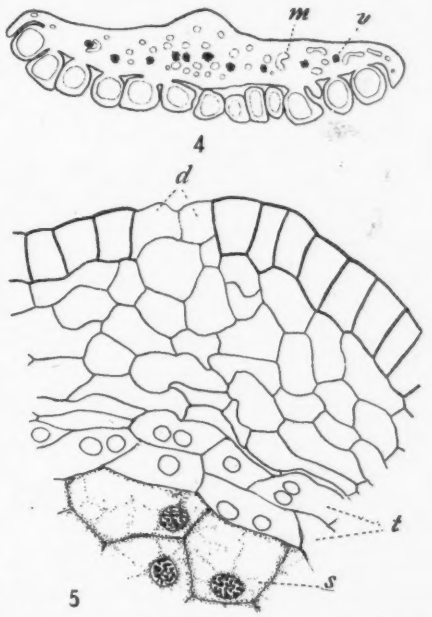
FIG. 3.—Staminate sporophylls: *a*, before dehiscence; *b*, dehiscence has taken place in the upper half but not yet in the lower; in *c*, nearly all the sporangia have shed their pollen; ×2.

The sporophylls appear to be arranged in vertical rows, and the number of sporophylls can be determined with considerable accuracy by counting the number of rows and number of sporophylls in a row, but the arrangement is strictly spiral. The lowest number of sporophylls observed was 72, in 8 rows with 9 in a row; and the highest number was 182, in 14 rows with 13 in a row; an average computed from 12 well developed cones was 11 rows with 11 in a row. The number of sporophylls, therefore, varies from 72 to 182, with 121 as an average; and the number of ovules varies from 144 to 364, with an average of 252, since each sporophyll bears two ovules.

The two hard spines or horns, which are similar to those on the microsporophyll, are always conspicuous, and they are so stiff and sharp that they make a large cone an uncomfortable object

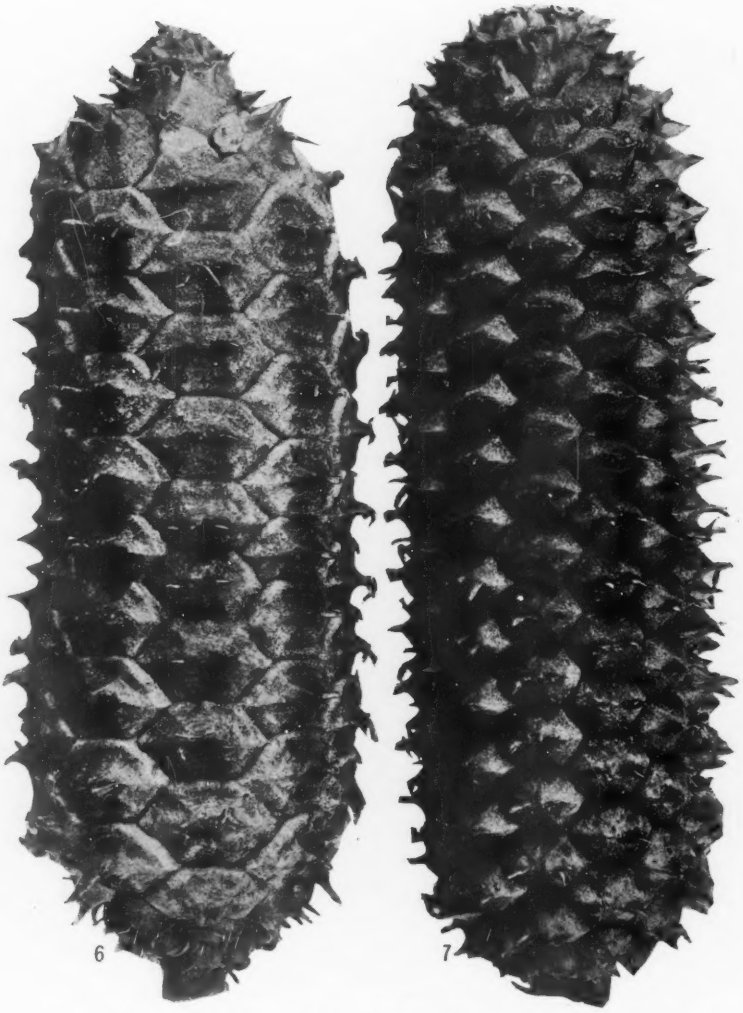
to hold in the hand. At the top of the cone the sporophylls often bear 3 spines and sometimes as many as 5 or 6, the arrangement and vascular connections making it evident that they are reduced pinnae. These sporophylls and some reduced sporophylls at the base of the strobilus bear no ovules.

The young ovules are softly pubescent, but become perfectly smooth at maturity. They are small, seldom reaching more than 2.6 cm. in length and 1.8 cm. in breadth. When very young, and also at maturity, they are white, but during intermediate stages there is a delicate pink color, not very conspicuous from the outside, because the color is in the layer which is to become stony, and consequently is masked by the outer fleshy layer. The stony layer is much thinner than in *Dioon*, and can be cut with a pocket knife, even when the seed is ripe. There is no pit in the base of the stony layer, as in *Dioon edule*, but rather a slight projection, so that the two species can be distinguished from each other by the character of the base of the stony layer.



FIGS. 4 AND 5.—Fig. 4, Transverse section of staminate sporophyll with its sporangia; *m*, mucilage ducts; *v*, vascular bundles; ×10; fig. 5, Portion of wall of microsporangium: *d*, dehiscence; *t*, tapetum; *s*, sporogenous tissue; ×375.

The general distribution of the vascular system of the ovule is as in *Dioon;* in the outer fleshy layer there is a system of unbranched bundles extending from the base of the ovule almost to the micropyle, and in the inner fleshy layer a system of bundles which branch



FIGS. 6 AND 7.—Fig. 6, ovulate strobilus with large sporophylls; ×½; fig. 7, ovulate strobilus with smaller and more numerous sporophylls; ×½.

dichotomously and occasionally anastomose. The number of bundles in the outer system varies from 8 to 10, with 9 as the most usual number. About 6 bundles pass through the stony layer to the inner fleshy layer, where they branch repeatedly. In the stalk of the sporophyll there is a single bundle passing toward each ovule; this bundle branches once in the spreading part of the sporophyll, and each branch contributes to both the inner and the outer vascular systems of the ovule.

Both strobili and ovules may reach the maximum size in greenhouse specimens where there has been no possibility of pollination. This seems to be the rule in *Ceratozamia*, although I have seen two or three greenhouse strobili in which nearly all the ovules were abortive.

The male gametophyte

Records in regard to the time of shedding pollen are not very complete. In two staminate cones sent from the Almolongo Valley, near Jalapa, December 5, 1906, arriving in Chicago December 12, the pollen tetrads had already shaken apart, but the exine had not begun to look yellow. In two cones sent from the same place February 5, 1907, and reaching Chicago 7 days later, the pollen was yellow, but the sporangia had not yet dehisced. Four cones from Chiltoyac, near Jalapa, reached Chicago March 10, 1906, and the largest of the four began to shed its pollen 2 days later. A cone of *Ceratozamia mexicana* var. *longifolia*, sent on April 14, 1909, from the Missouri Botanical Garden by Professor TRELEASE, reached Chicago the following day. Much of the pollen was already shed.

While there is considerable variation in the time at which the pollen is shed, the condition of the pollen at the time of shedding is always the same; there is a tube cell, a well developed, persistent prothallial cell, and a generative cell which will later give rise to the stalk and body cells.

The mature pollen grain of *Ceratozamia mexicana* can be distinguished from that of *Dioon edule* by the spore coats, the exine and intine being quite uniform throughout in *Ceratozamia*, while in *Dioon* the exine is much thicker at the base of the spore and the intine much thickened along the sides.

The pollen grain, as it is shed, is shaped like a kernel of coffee,

with a deep furrow across the top, due to the fact that the exine does not cover the entire surface, but is lacking at the apex of the spore, so that when the spore contracts in the drying out which precedes shedding, the elastic exine springs together until the opposite sides touch, thus making it look as if the exine covered the entire spore. When placed in water or in a nutrient solution, the spore immediately begins to swell, and in a few minutes becomes quite spherical. In a 10 per cent solution of cane sugar, or in the juice of either fresh or preserved pears, germination takes place at once. Within 24 hours the intine begins to protrude, and in 3 or 4 days some of the tubes are two or three times as long as the pollen grain. In cultures there is a considerable elongation of the pollen tube and some increase in the amount of starch, but I have never succeeded in finding a division of the generative cell. The beginning of germination, as it appears in a 10 per cent sugar solution, is shown in figs. 8, 9, and 10.

The pollen tube is quite characteristic, and easily distinguishes *Ceratozamia* from any cycads yet described. As in other cycads, the brown roof of the pollen chamber, with the nucellar beak in its center, is present, but the brown lines due to the haustoria of pollen tubes are scarcely visible, and even in abundantly pollinated strobili the brown spot itself is seldom more than 1 mm. in diameter. That there are haustoria, 2–3 mm. long and lying just beneath the surface of the nucellus, is evident from a glance at a section, but they do not cause conspicuous brown lines upon the surface.

The most striking feature of the pollen tube is a series of secondary haustoria developed from various parts of the enlarged basal end of the pollen tube (fig. 11). As soon as the pollen grain is shed, the primary haustorium, as the familiar haustorium of cycads might be called, begins to develop, and with little or no branching reaches a length of 1–2 mm., its course lying just beneath the surface of the nucellus. The secondary haustoria are developed much later. They have about the same diameter as the primary haustoria, but are more sinuous in outline and usually branch. Their general direction is toward the archegonia, and their development is so rapid that long before the division which is to form the ventral

canal nucleus and egg nucleus, while the archegonial chamber is still quite shallow and the pollen chamber only half way through the nucellus, their tips have already reached the megaspore membrane. They contain starch and occasionally the tube nucleus wanders into one of them, but the tube nucleus, at the stage shown in figs. 11 and 12, is almost invariably found in the enlarged portion of the tube and is usually near the body cell. Only in very early stages is it found in the primary haustorium.

As the tissue of the nucellus breaks down beneath the advancing pollen tubes, the secondary haustoria, especially those extending directly downward, become bent and twisted and finally appear as an irregular tangle pressing against the megaspore membrane (fig. 12). The tissues of the nucellus disorganize so rapidly that the secondary haustoria do not hold back the basal end of the tube, but advance with it. The disorganization which forms the pollen chamber is very extensive, including not only the region occupied by the basal ends of the tubes, but finally all the tissues in the region of the secondary haustoria.

The division of the generative cell into the stalk and body cells, a division which I was not able to secure in cultures, takes place quite promptly after the pollen grains have reached the pollen chamber, probably within a week after pollination. From a record of various cones of various seasons, the time at which the body cell divides shows considerable variation, the division being noted as early as the middle of June, and as late as the first of August. The most usual time is the first week in July.

In nearly all cases, two sperms are produced from each body cell, but four sperms were found in a few cases. In two cases, four sperms were found in isolated pollen tubes mounted without sectioning; in one case, four were found in one tube in serial sections; and in another case, shown in fig. 13, the body cell had divided, forming two cells, each with the aspect of a body cell and with two blepharoplasts, so that there is no doubt as to the manner in which the four sperms are formed.

At the division of the body cell, the mitotic figure is small and entirely intranuclear during the metaphase, but after the nuclear

membrane has broken down in the anaphase, the spindle develops enormously and occupies a broad zone between the two daughter nuclei (fig. 14).

The two cells formed at this division are sperm mother cells, as we have already shown in case of *Dioon edule* (4). In each of the sperm mother cells a sperm is formed, and subsequently escapes by the breaking down of the wall of the mother cell (fig. 15).

The blepharoplast is the largest yet recorded for any cycad, seldom measuring less than 20 μ in diameter, and occasionally reaching a diameter of 27 μ, while blepharoplasts 25 μ in diameter are not rare. The enormous size of this blepharoplast will be appreciated when one remembers that nuclei in the meristematic region of the familiar onion root tip (*Allium Cepa*) seldom measure more than 15 μ in diameter and rarely reach a diameter of 20 μ. Naturally, this blepharoplast is favorable for study, and from the collections of six years the series of stages is very complete, but since such a study should be strictly cytological, I shall reserve for a special paper the division of the body cell and the behavior of the blepharoplast in the formation of the ciliated spiral band. During the formation of the spiral band, remarkable changes take place in the nucleus of the sperm, and these will also be considered in the special paper. For the present, we need only say that the solid blepharoplast becomes vacuolated, and breaks up into a mass of granules from which the greater part of the ciliated band is formed. The band starts in contact with the nucleus, the lowest turn being formed first, and ends at the apex of the sperm. The most usual number of turns of the spiral band is 7, but 6 and also 7.5 are found occasionally. The spiral may be either right or left, or better, it may be formed either in the direction of the hands of a clock or contra clockwise. The actual direction is usually with the hands of the clock, but camera lucida drawings will show the contra clockwise spiral, since the microscopic image is always reversed. In many instances it was possible to determine the direction of the spiral in both of the two sperms from the same body cell, and in most cases one showed the clockwise and the other the contra clockwise direction.

The sperms of *Ceratozamia* are not so large as those of *Zamia* or

Dioon, the average measurements of sperms in the pollen tube being 220 μ in diameter and 185 μ in length from apex to base. The sperms of *Zamia floridana*, as described by WEBBER (5), reach a diameter of 306 μ and a length of 332 μ, and those of *Dioon edule* measure 230 μ in diameter and 300 μ in length. The sperms of *Cycas* and *Microcycas* are smaller.

The sperms were often examined in the living condition. They are easily visible to the naked eye, and with a pocket lens one can see the more general features of their movements, but an examination under low powers of the microscope is more satisfactory. When exposed to the air, the pollen tubes soon burst, the sperms seldom swimming longer than 15 minutes after the ovules are opened, but when the ovules are cut transversely, the female gametophyte removed, and the cut end placed in a drop of sugar solution on a slide, the tubes may be examined for a few seconds at a time and thus allow a more prolonged observation. Just how long the sperms are in the motile condition was not determined, for sperms which have not begun to move when an ovule is opened may suffer from the shock, and when sperms are already moving it cannot be determined how long they have been motile. Movements of individual sperms have been observed for 6 hours.

The movements are like those described for *Dioon edule*, a forward movement accompanied by a rotation upon the axis. The sperms swim rapidly, bumping against each other and against the sides of the tube. When swimming straight ahead the apex is stretched out in front (fig. 16), but when the sperm strikes anything the apex is often drawn in suddenly, with a movement reminding one of the sudden retreat of a *Vorticella*. So far as the form is concerned, the drawings of three sperms shown in figs. 15 and 16 might have been made from a single sperm at intervals of a few seconds. There is also a slower, amoeboid movement of both cytoplasm and nucleus. The contour of the nucleus is very irregular and is constantly changing. Slender prolongations of the nucleus may reach nearly or quite to the ciliated band.

A few attempts were made to determine whether the sperms are chemotactic or not, but no results were obtained. MIYAKE (8) reported that the sperms of *Cycas* show no chemotropism, and

while his results were negative, I am inclined to believe they are entirely correct, for the entrance of the sperm into the egg in both *Ceratozamia* and *Dioon* seems to be independent of any chemotactic phenomena.

The female gametophyte

If strobili were numerous, *Ceratozamia* would be favorable for a study of the origin and development of the megaspore, for the strobili break through the bud scales at a very early stage. The earliest stage in any material shows free nuclear division in the megaspore. The general course of development is about the same as in *Dioon edule* (**9**), the principal differences being that structures are smaller, the mature gametophyte being about 2.5 cm. in length, and the archegonia at the time of fertilization seldom reaching a length of more than 3 mm.

WARMING (**10**) in 1877 reported a ventral canal cell in *Ceratozamia robusta*, but soon concluded that he had been mistaken. It is not surprising that he was in doubt, for the ventral canal nucleus in *Ceratozamia mexicana* is very small and usually disorganizes very promptly. The relative sizes of the ventral canal nucleus and the egg nucleus are shown in fig. 17, while 17*a* is a detailed drawing of the ventral canal nucleus shown in fig. 17. It is of special interest to note that the ventral canal nucleus does not always disorganize, but may enlarge, as it sometimes does in *Pinus* (**11**) and *Ginkgo* (**12**), and in such cases it is very probable that the egg may be fertilized by the ventral canal nucleus. I have seen two cases in *Ceratozamia* in which a large nucleus, looking like the nucleus of the sperm, was only a short distance from the egg nucleus, but no ciliated band could be found in the egg and the neck cells were still turgid. The objection is easily made that the failure to find the ciliated band is only negative evidence, but the band is so large and so persistent, that to one familiar with cycads the failure to find it at this early stage is conclusive proof that no band is present. Of course it might be suggested that only the nucleus had entered the egg, the band remaining outside, but in many cases the sperm, with the ciliated band, was observed inside the egg, sometimes being plainly visible in late free nuclear stages of the proembryo (fig. 20).

A strong reason for believing that fertilization is sometimes effected by a ventral canal nucleus is found in a paper by VAN TIEGHEM (**13**) published in 1870. He secured four seedlings, the result of fertilization of the ovules of *Ceratozamia longifolia* by "the pollen of *C. mexicana*, which had been preserved for three years." VAN TIEGHEM speaks of these seedlings as hybrids, but I do not believe the pollen of *Ceratozamia* will live for three years. Pollen of *C. mexicana*, shed April 22, 1909, in cultures started on that date and also a week later, germinated immediately, but in cultures made a month later from the same collection of pollen, the grains simply became spherical, but would not germinate. In January 1911, I pollinated two cones of *Zamia Ottonis* with some of the same pollen, at about the same time pollinating another cone of *Z. Ottonis* with pollen of *Z. floridana*. I have not yet examined the cones, except to note that they are in fine condition, preferring to wait for the later embryo and seedling stages, if there should be any. At the time of this pollination I again made cultures of the old pollen of *Ceratozamia*, but not a single pollen grain germinated, and recently I repeated the attempt, but no germination occurred. The old pollen is doubtless dead, and VAN TIEGHEM'S seedlings were parthenogenetic or were the result of fertilization by a ventral canal nucleus. I might mention here that I have preparations of *Encephalartos* from a greenhouse specimen where there had been no possibility of pollination, in which the ventral canal nucleus has become greatly enlarged and has moved toward the egg nucleus. I should not be surprised to find occasional seedlings from cycads in greenhouses where there has been no pollination.

The archegonial chamber is conspicuous before the pollen tubes are half way through the nucleus, and during the early stages in its development it contains a fluid, doubtless secreted by the gametophyte, for the megaspore membrane is torn loose from the bottom of the chamber. At the time of fertilization the chamber, although moist, does not contain liquid.

The megaspore membrane is thin, only 2.5–3 μ in thickness. It has about the same structure as in *Dioon edule* (**9**), a comparatively homogenous inner layer beset with an outer layer of irregular club-shaped bodies. These bodies, which in some gymnosperms

are prismatic on account of pressure, are so scattered that they are nearly always round in vertical view (fig. 18).

FERTILIZATION

All observations indicate that fertilization takes place as in *Dioon edule*, the liquid from the pollen tube lowering the turgidity of the neck cells of the archegonium, so that they allow the escape of a portion of the cytoplasm of the upper part of the egg, thus producing a vacuole which draws the sperm into the egg.

In numerous instances the sperms were observed within the egg, occasionally two or three sperms entering the same egg, but in such cases the extra sperms remain at the top of the egg, and the nuclei do not slip out from the cytoplasmic sheath. The actual fusion of the sperm and egg nuclei was not observed, and consequently it cannot be stated at present whether they fuse in the resting condition or behave as in *Pinus*.

Embryo

The extent of the free nuclear period in the development of the embryo was not determined, the latest stage observed being the 256-nucleate stage shown in fig. 19. No stages were found between this and the young embryos with suspensors shown in figs. 20–22.

The membrane of the egg, often with traces of the archegonium jacket clinging to it, persists for a long time. Five such membranes, each with a suspensor coming from its base, are shown in fig. 20. In this case four of the suspensors, each with an embryo at its tip, have united, forming a single suspensor with a single embryo. The other suspensor, with its embryo, advanced only half as far before it ceased to develop. In another case (fig. 21), two suspensors with their embryos have united, and the third, although smaller, has reached about the same length. In another case (fig. 22), all the suspensors and embryos developed separately. These cases are characteristic. A single embryo may be the product of one fertilization or may come from several eggs. In early stages, the young embryos are more or less irregular (fig. 23), but regularity is soon established.

The strobili disorganize and shed their seeds very early, often

before the stage shown in figs. 20–23 is reached, and consequently before the cotyledons have begun to be differentiated. Sister HELEN ANGELA (14), noting this fact and finding traces of vascular tissue which might belong to the missing cotyledon, rotated seeds on a klinostat from the time the seeds were liberated until the embryos were mature. Such seeds showed two cotyledons as in other cycads, so that the single cotyledon of *Ceratozamia*, as it is found in nature, is due to a suppression of one of the cotyledons, doubtless on account of the early liberation of the seeds.

The seeds of *Ceratozamia* germinate as soon as they are ripe, a feature which I have noted in *Dioon edule*, *D. spinulosum*, *Zamia floridana*, *Cycas circinalis*, *Macrozamia Fraseri*, and *Stangeria paradoxa*. Very probably the seeds of all cycads may germinate without any resting period; but seeds of *Ceratozamia*, which had become dry in the laboratory, were planted a year later and germinated readily. Seeds of *Dioon edule* which had been in the laboratory for nearly three years germinated. The most favorable time for germination is that immediately following maturity, for at this time nearly all seeds of both *Ceratozamia* and *Dioon* will germinate, but after a lapse of a few months the proportion of seeds which will germinate steadily diminishes.

Summary

1. *Ceratozamia mexicana* grows best in well shaded mesophytic conditions.

2. Any individual in passing from the seedling to the adult stage shows such a progressive change in its leaves, the leaflets becoming larger, broader, thicker, and more numerous, that descriptions of species based largely upon leaves are open to suspicion.

3. The ovulate strobilus shows considerable variation in the size and number of its sporophylls.

4. In addition to the primary haustorium, a system of secondary haustoria is developed later from the basal portions of the pollen tube. There are regularly two sperms, but occasionally four are produced.

5. A small ventral canal nucleus is present, but occasionally it enlarges and may fertilize the egg. It is suggested that this

may explain the so-called hybrids obtained by VAN TIEGHEM. In most cases fertilization occurs in the usual way.

6. Both suspensors and young embryos may unite, so that from five fertilized eggs there may come one to five embryos. In the mature seed, as found in nature, there is one embryo with a single cotyledon.

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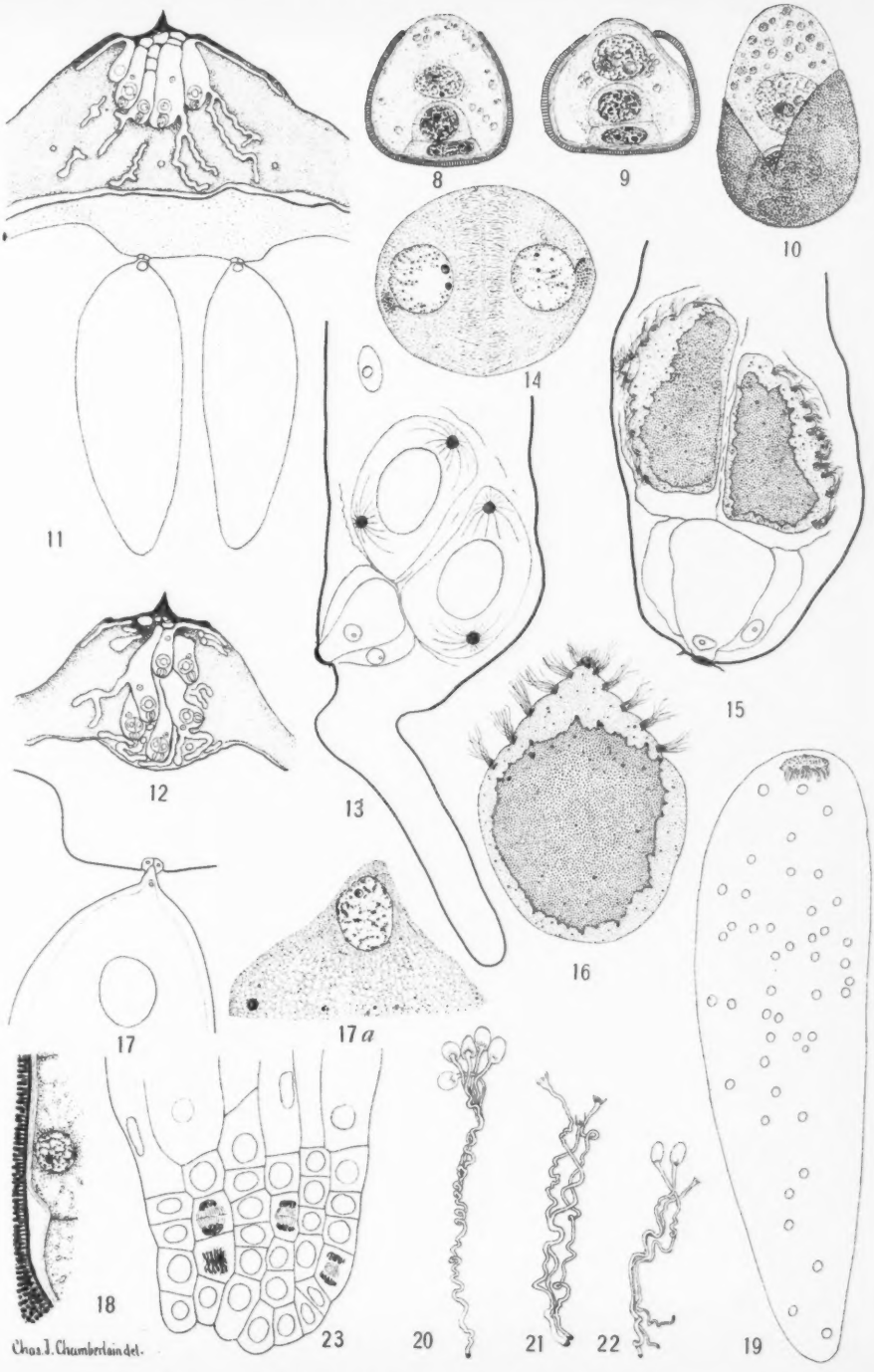

CHAMBERLAIN on CERATOZAMIA

EXPLANATION OF PLATE I

(Figs. 1–7 are text cuts)

Ceratozamia mexicana

FIG. 8.—Pollen grain beginning to germinate in a sugar solution; beneath the tube nucleus is the generative cell which is to produce the stalk and body cells; beneath this and resting upon the intine is the single persistent prothallial cell; the spherical bodies are starch grains; ×730.

FIG. 9.—Like the preceding figure, but there has been some plasmolysis, and at the right side of the figure, toward the top, the intine has pulled loose from the exine; ×730.

FIG. 10.—Germinating pollen grain drawn from living material; ×730.

FIG. 11.—Nucellus and part of female gametophyte with archegonia; the pollen tube at the right shows the primary haustorium just beneath the upper surface of the nucellus, and farther down, opposite the body cell, a branching secondary haustorium; the lightly dotted area above the archegonia represents the liquid filling the archegonial chamber and pressing up the megaspore membrane, represented by the dark line; ×14.

FIG. 12.—Nucellus at a later stage showing behavior of secondary haustoria; ×14.

FIG. 13.—Pollen tube which would have produced four sperms; a single unbranched secondary haustorium extends obliquely downward; ×130.

FIG. 14.—Two young sperm mother cells showing the remnants of the broad spindle and the ciliated band just beginning to form; ×180.

FIG. 15.—Two sperms about to escape from their mother cells; ×130.

FIG. 16.—Mature sperm; ×180.

FIG. 17.—Part of archegonial chamber and upper part of the archegonium, showing the small ventral canal nucleus and the egg nucleus; ×25.

FIG. 17*a*.—Detailed drawing of the ventral canal nucleus shown in the preceding figure; ×475.

FIG. 18.—Megaspore membrane with parts of two adjacent endosperm cells; ×833.

FIG. 19.—Free nuclear stage of proembryo; the sheath and ciliated band of the sperm are shown at the top; ×27.

FIG. 20.—One embryo formed by the fusion of four; the fifth embryo stopped developing part way down the suspensor region; ×1.5.

FIG. 21.—Three suspensors with two embryos; ×1.5.

FIG. 22.—Each suspensor has an embryo at its tip; ×1.5.

FIG. 23.—Young embryo showing irregular outline of an embryo formed by fusion of two or more embryos; ×1.5.

THE WILTING COEFFICIENT AND ITS INDIRECT DETERMINATION[1]

LYMAN J. BRIGGS AND H. L. SHANTZ

THE WILTING COEFFICIENT

If the roots of a plant are well established in a mass of soil, the plant gradually reduces the water content until permanent wilting occurs. The water remaining in the soil under this condition has been termed non-available by previous writers. We have found, however, that plants can reduce the soil moisture content somewhat below the point corresponding to the permanent wilting of the leaves, so that the water content at the wilting point is not strictly non-available. In fact, this loss of water from the soil to the air goes on through the plant tissues even after the death of the plant, and appears to be limited only by the establishment of a state of equilibrium between the soil and the air. The plant during the drying stage acts simply as a medium for the transference of water, and while the rate of loss is reduced, the final result is the same as if the air and soil were in direct contact. By means of the wax seal method, which effectually prevents all direct loss of water from the soil, we have been able to demonstrate conclusively that there is a continued loss of water from the soil through the plant long after wilting occurs. This is shown by the results given in the accompanying table (table I).

The wheat seedlings were grown in sealed glass pots containing about 200 grams of soil. The second column of the table gives the water content of the soil corresponding to the wilting of the plants. The third column gives the number of days intervening between the wilting and the death of the plants, at which time the moisture content of the soil had been materially reduced, as shown in the fourth column. A still greater loss of water occurred during the subsequent period, at the end of which the moisture content of the

[1] Published by permission of the Secretary of Agriculture.

soil had been reduced to the point indicated in the last column of the table. The mean moisture content of the soil at the death point had been reduced to 85 per cent of the water content at the wilting point, while the mean soil moisture content at the end of the experiment was only 63 per cent of that at the wilting point.

TABLE I

THE WATER CONTENT OF THE SOIL IN SEALED POTS AT THE WILTING POINT AND DEATH POINT FOR KUBANKA WHEAT, AND AT A LATER PERIOD

Pot no.	Wilting point	Time interval in days	Death point	Time interval in days	Final percentage
4.....	7.0	28	5.2	126	3.1
6.....	7.9	25	5.9	126	2.6
7.....	7.0	25	5.5	126	3.5
8.....	6.6	19	6.4	126	4.9
9.....	7.1	27	5.9	134	4.8
10.....	7.8	27	6.9	134	5.9
11.....	6.9	19	5.9	126	4.3
12.....	7.3	27	6.6	134	5.9
13.....	8.0	27	6.9	37	6.1
14.....	7.3	27	6.2	134	4.9
Mean ...	7.3		6.2		4.6

The water remaining in the soil at the time the plant wilts cannot then with propriety be termed "non-available." We have shown that a considerable part of it is available, being absorbed by the roots of the dying or dead plant and evaporated from its aerial tissues, this process becoming slower and slower as the water content is reduced, and reaching its final limit in a condition of equilibrium between the soil and the air.

It appears advisable, therefore, to use a more specific term for the moisture content of the soil corresponding to the wilting point of a plant, and we have employed the term "wilting coefficient" in this sense in the present paper. The wilting coefficient is defined then as the percentage water content of a soil when the plants growing in that soil are first reduced to a wilted condition from which they cannot recover in an approximately saturated atmosphere without the addition of water to the soil.

The method used in determining the wilting coefficient has been

described in a previous paper.[2] The plants are grown in small glass pots, evaporation from the soil surface being prevented by means of a wax seal. The conditions are maintained as nearly uniform as possible until the plants wilt permanently. Special care is taken to secure uniformity in the texture and water content of the soil mass before filling the pots. Sudden fluctuations in soil temperature are avoided by keeping the pots in a water bath during the growth of the plants. When these precautions are observed, the physiological measurement of the wilting coefficient is as accurate as the physical methods of measuring the moisture retentiveness of a soil. It is shown in the paper already referred to that the probable error of the mean wilting coefficient for 13 or more determinations is only about 0.005 of the actual determinations in the case of loam and clay soils. For single determinations the probable error is about 0.02 of the mean value. In the case of sands, the corresponding probable error is about twice as great as in the loam and clay soils.

INDIRECT DETERMINATION OF THE WILTING COEFFICIENT

In all plant investigations in which the water supply may become a limiting factor, it is necessary to determine from time to time the amount of moisture in the soil available for plant growth. If we make the specific assumption that growth cannot take place unless the water content of the soil is equal to or exceeds the wilting coefficient, then the percentage of soil moisture available for growth at any time is represented by the actual moisture content minus the wilting coefficient. If the actual water content is less than the wilting coefficient, then the percentage of available water is negative, that is, water to this amount must be added to the soil before any growth can take place.

The percentage of moisture in the soil at the wilting point varies greatly in different types of soil. This appears to have been established first by SACHS,[3] and has been further investigated

[2] BRIGGS, L. J., and SHANTZ, H. L., A wax seal method for determining the lower limit of available soil moisture. BOT. GAZ. 51:210–219. 1911; also The wilting coefficient for different plants and its indirect determination. U.S. Dept. Agric., Bur. Pl. Ind., Bull. 230. 1911.

[3] SACHS, J., Bericht über die physiologische Thätigkeit an der Versuchstation in Tharandt. Landw. Versuchs-Stat. 1:235. 1859.

by GAIN,[4] HEINRICH,[5] and more recently by HEDGCOCK.[6] No quantitative correlation between the soil texture and the non-available moisture was established, and only in the case of a few soil types was the non-available moisture recorded.

In field studies of soil moisture, determinations of the total water content can easily be made. The errors which enter into the determination of the wilting coefficient under field conditions are very great, due to the direct evaporation from the soil, local variation in soil texture, and non-uniform root distribution, combined with the difficulty of determining the exact wilting point when the roots occupy a large soil mass. Furthermore, it is only during periods of extreme drought that conditions are favorable for wilting coefficient determinations in the field. In view of these difficulties, it becomes important to ascertain whether the wilting coefficient can be determined by an indirect method based upon the relationship of the wilting coefficient to the moisture retentiveness of the soil as measured by physical methods.

Accordingly we have compared the wilting coefficient with the moisture equivalent, the hygroscopic coefficient, the moisture holding capacity, and mechanical analysis for a series of soils ranging from sands to clays. In the wilting coefficient determinations Kubanka wheat (Grain Investigations no. 1440) has been used as an indicator. The results of these comparisons are given in the following sections:

RELATION OF THE WILTING COEFFICIENT TO THE MOISTURE EQUIVALENT

The moisture equivalent of the soil is the percentage of water which it can retain in opposition to a centrifugal force 1000 times that of gravity.[7] In making the determinations the soils are

[4] GAIN, E., Action de l'eau du sol sur la végétation. Rev. Gén. Botanique 7:73. 1895.

[5] HEINRICH, R., Zweiter Bericht über die Verhältnisse und Wirksamkeit des Landwirtschaftlichen Versuchs-Station zu Rostock, 1894, p. 29.

[6] HEDGCOCK, G. G., The relation of the water content of the soil to certain plants, principally mesophytes. Bot. Survey Nebraska. VI. Studies in the vegetation of the State II. 1902:5–79.

[7] BRIGGS, L. J. and MCLANE, J. W., The moisture equivalent of soils. U.S. Dept. Agric., Bur. Soils, Bull. 45. 1907; also, Moisture equivalent determinations and their application. Proc. Amer. Soc. Agronomy (1910) 2:138–147. 1911.

placed in perforated cups and moistened with an amount of water in excess of the amount they can hold in opposition to the centrifugal force. After standing 24 hours, the cups are placed in a centrifugal machine, which is operated at a constant speed so chosen as to exert a force 1000 times that of gravity upon the soil moisture. Each soil then rapidly loses water until the capillary forces are increased sufficiently to establish equilibrium with the centrifugal force employed. The moisture content of each soil is now not only in equilibrium with a force 1000 times that of gravity, but is also in capillary equilibrium with every other soil which has been similarly treated, so that if the soils are placed in capillary contact in any combination whatever, no movement of water from one soil to another will occur. The moisture content of each soil under these conditions is the moisture equivalent of that soil. This method, then, provides a means of determining and comparing the retentiveness of different soils for moisture when acted upon by a definite force, which is measured in absolute terms and is reproducible within narrow limits.

In the accompanying table (table II) is given a comparison of the wilting coefficient and the moisture equivalent for a series of soils ranging in texture from a coarse sand to a clay. The names applied to the soils have been determined from the mechanical analyses in accordance with the soil classification table used by the Bureau of Soils.[8] The soils are arranged in the order of increasing moisture equivalents. For the moisture equivalent determinations we are indebted to Mr. J. W. McLane. All moisture determinations are expressed as percentages of the dry weight of the soil used.

The moisture equivalent determinations given in the table represent in each case the mean of two determinations. The number of wilting coefficient determinations made upon each soil is shown in the fourth column, and the mean of these determinations is given in the fifth column. The last column gives the ratio of the moisture equivalent to the wilting coefficient for each soil.

It will be seen from an inspection of the table that the soils used in the comparison show a wide range in moisture retentiveness,

[8] Soil Survey Field Book, 1906.

the moisture equivalent increasing from 1.6 per cent in sand to over 30 per cent in the clay loam; while the wilting coefficient ranges from 0.9 per cent in sand to 16.5 per cent in the clay loam. The mean ratio of the moisture equivalent to the wilting coefficient for all the soils examined is 1.84. The probable error of this mean is ±0.013; that is to say, considering the series to be representative of soils as a whole, the chances are even that if a similar series of determinations were made the mean of the ratios would fall between 1.827 and 1.853.

TABLE II

THE RELATION OF THE WILTING COEFFICIENT TO THE MOISTURE EQUIVALENT IN SOILS RANGING FROM SAND TO CLAY

No.	Soil type	Moisture equivalent	Wilting coefficient		Ratio of moisture equivalent to wilting coefficient
			No. dets.	Average	
7	Coarse sand	1.6	11	0.9	1.78
2	Fine sand	4.7	16	2.6	1.81
8	Fine sand	5.5	3	3.3	1.67
9	Fine sand	6.7	2	3.6	1.86
3	Sandy loam	9.7	9	4.8	2.02
10	Sandy loam	11.9	3	6.3	1.89
4	Fine sandy loam	18.1	13	9.7	1.87
12	Loam	18.9	3	10.3	1.83
A	Sandy loam	19.6	1	9.9	1.98
B	Fine sandy loam	19.9	1	10.8	1.84
C	Fine sandy loam	22.1	1	11.6	1.90
5	Loam	25.0	12	13.9	1.80
D	Loam	27.0	1	15.2	1.78
13	Clay loam	27.4	2	14.6	1.88
14	Clay loam	29.3	4	16.2	1.81
E	Clay loam	30.0	1	16.5	1.82
6	Clay loam	30.2	16	16.3	1.85

Mean...1.84

Probable error of mean.....±0.013

It will be noted that the greatest departures in the ratios are found among the sandier soils. This is due to the fact that a slight experimental error in determining either the moisture equivalent or the wilting coefficient affects the ratio markedly owing to the small percentages of moisture with which we are dealing in these soils.

The significant feature of the results here presented is the fact that through the wide range of moisture retentiveness exhibited

by the soils employed, the ratio of the moisture equivalent to the wilting coefficient appears to be constant within the limits of experimental error. In other words, two determinations of the moisture retentiveness of these soils, one physical and the other physiological, show a linear relationship which is independent of the texture of the soil. The relationship is expressed by the following formula:

$$\frac{\text{Moisture equivalent}}{1.84 \pm 0.013} = \text{wilting coefficient.}$$

In order to compare the available moisture content of one soil with that of another, we must know or be able to estimate accurately the wilting coefficient of each soil. The minimum limit of moisture available for growth is the datum line from which all comparisons should be made. This datum can be established directly by wilting coefficient measurements, or it can now be calculated by means of the ratio just established. The latter method for field work is far simpler and more expedient. The soil sample taken in the field for soil moisture determination, although ample for duplicate measurements of the moisture equivalent, is usually not large enough for a single wilting coefficient determination. Moreover, the period of time required for wilting coefficient determinations, combined with the uncertainty which accompanies all physiological work when duplication is impossible, makes this determination less expedient and the results in such cases less reliable than those derived from the moisture equivalent by the use of the ratio here established.

The relationship established between the wilting coefficient and the moisture equivalent led us to believe that a similar relationship might be found for some of the other physical measurements of soil moisture retentivity. We have accordingly made similar comparisons of the wilting coefficient with the hygroscopic coefficient, the moisture holding capacity, and the soil texture, as expressed by mechanical analysis. The last mentioned determination does not measure moisture retentivity, but it does measure certain properties of the soil which determine the moisture retentivity to a large extent. We will now consider the results of these comparisons.

THE RELATION OF THE WILTING COEFFICIENT TO THE HYGROSCOPIC COEFFICIENT

When a dry soil is placed in a saturated atmosphere, it will absorb water vapor until a condition of approximate equilibrium is attained. The moisture content of a soil under such conditions is known as the hygroscopic coefficient of that soil.

The determination of the hygroscopic coefficient, unless carried out with special precautions, is not very exact. It is influenced by variation in temperature and by any departure from a condition of complete saturation of the surrounding air.[9] The time element is also an important factor, since the soil absorbs water very slowly, particularly near the point of equilibrium. In fact, equilibrium would not be theoretically obtained until the interstitial spaces of the soil were practically filled with water. The method thus has certain inherent disadvantages which are not encountered in moisture equivalent determinations.

The hygroscopic moisture determinations given in this paper were carried out in a double-walled ice chest kept in a subterranean room, where the temperature was approximately 20 C°.[10] The bottom of the chest was covered with water and the zinc walls were lined with blotting paper which was kept saturated.

A comparison of the hygroscopic coefficient and the wilting coefficient for a number of soils is given in the accompanying table (table III). The soils used are the same as those employed in the preceding experiments, being arranged in order of increasing moisture equivalents.

The hygroscopic determinations given in the table are the mean of duplicate measurements. The determinations range from 0.5 per cent in sand to 13.2 per cent in clay loam. The corresponding wilting coefficients have been discussed in connection with the preceding table.

The ratio of the hygroscopic coefficient to the wilting coefficient is given for each soil in the last column of the table. The mean of this ratio is 0.68, with a probable error of ±0.012. We have,

[9] HILGARD, E. W., Soils. 1906. p. 196.

[10] Determinations by J. W. MCLANE.

then, in this ratio a second method of determining the wilting coefficient, when the hygroscopic coefficient is known, as follows:

$$\frac{\text{Hygroscopic coefficient}}{0.68 \pm 0.012} = \text{wilting coefficient.}$$

HEINRICH[11] determined the non-available moisture in six types of soil, using the wilting points of corn and oats as indicators. He

TABLE III

THE RELATION OF THE WILTING COEFFICIENT TO THE HYGROSCOPIC COEFFICIENT IN SOILS RANGING FROM SAND TO CLAY

No.	Soil type	Hygroscopic coefficient	Wilting coefficient		Ratio of hygro. coefficient to wilting coefficient
			No. dets.	Average	
7	Coarse sand	0.5	11	0.9	0.556
2	Fine sand	1.5	16	2.6	0.577
8	Fine sand	2.3	3	3.3	0.698
9	Fine sand	2.3	2	3.6	0.639
3	Sandy loam	3.5	9	4.8	0.729
10	Sandy loam	4.4	3	6.3	0.699
4	Fine sandy loam	6.5	13	9.7	0.670
12	Loam	7.8	3	10.3	0.757
A	Sandy loam	6.3	1	9.9	0.636
B	Fine sandy loam	6.6	1	10.8	0.611
C	Fine sandy loam	7.5	1	11.6	0.646
5	Loam	9.8	12	13.9	0.705
D	Loam	9.6	1	15.2	0.631
13	Clay loam	11.8	2	14.6	0.808
14	Clay loam	13.2	4	16.2	0.815
E	Clay loam	11.2	1	16.5	0.679
6	Clay loam	11.4	16	16.3	0.700
				Mean...	0.680
				Probable error of mean.....	±0.012

also measured the hygroscopic coefficient of each soil used in his experiments. We have computed from his measurements the mean ratio of the hygroscopic coefficient to the wilting coefficient, together with the probable error of the mean, obtaining the value 0.696 ± 0.03, as compared with the ratio 0.68 ± 0.01 obtained from our experiments. While HEINRICH's determinations show more variation than our own, the ratio obtained from his results agrees within the limits of his probable error with the ratio obtained in

[11] HEINRICH, R., *l.c.* 28–32.

our experiments. A single determination by ALWAY,[12] in which barley plants were used, gave a ratio of 0.65.

In the absence of a more definite relationship between non-available moisture and the hygroscopic coefficient, ALWAY[13] has advocated deducting the hygroscopic coefficient from the field soil moisture determinations as a basis for comparing the available moisture in soils. Our measurements, however, show that the wilting coefficient is about 1.47 times the hygroscopic coefficient, so that very misleading results may be obtained from this approximation, particularly when the moisture supply is limited. For example, consider two soils containing respectively 14.7 per cent and 20 per cent of water and each having a hygroscopic coefficient of 10 per cent. Under these conditions all the water in the first soil is practically non-available for growth, while the second contains over 5 per cent of available moisture. Simply deducting the hygroscopic coefficient would lead to the erroneous conclusion that both soils contained considerable available moisture.

It is important in this connection to distinguish clearly between the hygroscopic coefficient, as used above, and the hygroscopic water content, which is simply the water content of "air-dry" soil. The latter term has recently been used by DUGGAR,[14] who, in discussing HEINRICH'S results as given by CAMERON and GALLAGHER,[15] says: "It will be noticed that so soon as the amount of water in ordinary soil becomes about three times the hygroscopic water content, it begins to assume physiological importance." The water content of air-dried soil may vary according to atmospheric conditions from practically zero in the case of some sun-dried desert soils to the hygroscopic coefficient

[12] ALWAY, F. J., Soil studies in dry land regions. Bur. Plant Industry, Bull. 130. 17–42. 1908.

[13] ALWAY, F. J., Studies of soil moisture in the "Great Plains" region. Jour. Agric. Sci. 2:334. 1908.

[14] DUGGAR, B. M., Plant physiology. 1911, pp. 56, 57.

[15] CAMERON, F. K., and GALLAGHER, F. E., Bureau of Soils, U.S. Dept. Agric., Bull. 50, pp. 57, 58. An error occurs in CAMERON and GALLAGHER'S paper in connection with HEINRICH'S results. They give his determinations on air-dried soils, but state that these determinations were made after exposing the soils to a saturated atmosphere for a week.

when exposed in a saturated atmosphere. There is consequently nothing definite or reproducible about such determinations, unless the conditions under which the measurements were made are also known, and any ratio derived from such measurements is likely to give misleading results when applied to other determinations.

THE RELATION OF THE WILTING COEFFICIENT TO THE SATURATION COEFFICIENT AND THE "MOISTURE HOLDING CAPACITY" OF SOILS

The saturation water content or the saturation coefficient is the percentage of water held in the soil when all interstitial space is filled with water. The "moisture holding capacity" is the percentage of water a soil can retain in opposition to the force of gravity when free drainage is provided. This is dependent upon the height of the soil column employed, diminishing as the height of the column is increased.[16] When the soil column is made very short, for example 1 cm. in height, the two determinations are practically identical. Both are greatly influenced by the packing and the granulation of the soil, so that determinations are subject to wide variation in the hands of different observers.

In the accompanying table (table IV) the wilting coefficients of a series[17] of soils are compared with the moisture holding capacity. Following HILGARD,[18] the latter determinations were made with a soil column 1 cm. in height, with free drainage.

The moisture holding capacity of the soils used in the comparison ranged from 23 to 71 per cent. In this case the ratio between the moisture holding capacity and the wilting coefficient is not constant. However, an approximately constant relationship is obtained if the moisture holding capacity is first reduced by 21. The ratio of the moisture holding capacity less 21 to the wilting coefficient is shown in the last column of the table. The mean ratio for the 15 soils

[16] HILGARD, E. W., and LOUGHRIDGE, R. H., Rept. Calif. Sta. 1892–94.
BRIGGS, L. J., Mechanics of soil moisture. U.S. Dept. Agric., Div. of Soils, Bull. 10. 1897.

[17] In this work it was not possible to secure samples of all the soils used in the preceding experiments.

[18] HILGARD, E. W., Soils. 1906, p. 209.

examined is 2.90±0.06. The relationship between the wilting coefficient and the moisture holding capacity is then:

$$\frac{\text{Moisture holding capacity} - 21}{2.9 \pm 0.06} = \text{wilting coefficient.}$$

TABLE IV

RELATIONS OF THE WILTING COEFFICIENT TO THE MOISTURE HOLDING CAPACITY

No.	Soil type	Moisture holding capacity percentage	Wilting coefficient percentage	Ratio of moisture holding capacity −21 to wilting coefficient
7	Coarse sand	23.2	0.9	2.44
2	Fine sand	29.9	2.6	3.40
8	Fine sand	28.5	3.3	2.27
9	Fine sand	31.4	3.6	2.84
F	Sandy loam	44.9	8.3	2.88
G	Sandy loam	50.1	9.5	3.06
H	Loam	55.9	11.0	3.17
I	Loam	58.6	11.6	3.24
J	Loam	59.8	11.7	3.30
86	Clay loam	54.2	13.8	2.40
K	Clay loam	58.2	14.7	2.52
L	Clay loam	63.2	14.9	2.83
M	Clay loam	71.3	15.0	3.35
N	Clay loam	67.2	15.7	2.94
O	Clay loam	69.5	16.7	2.90
			Mean	2.90
			Probable error of mean ratio	±0.06

RELATION OF WILTING COEFFICIENT TO SOIL TEXTURE AS EXPRESSED BY MECHANICAL ANALYSIS

Soil texture has been more extensively used than any other physical property for the quantitative description of soils, and unfortunately it has been one of the most difficult to interpret from the standpoint of moisture retentiveness. Texture is quantitatively expressed by means of the mechanical analysis, which shows the composition of the soil when the particles are separated into groups according to size. The accuracy with which the texture of the soil can be expressed by this means is dependent upon the number of groups into which the particles are separated. But the difficulty of securing a complete separation of the finer particles into the desired groups places a practical limit upon the number of groups, which is usually limited to seven.[19]

[19] BRIGGS, L. J., MARTIN, O. F., and PEARCE, J. R., The centrifugal method of mechanical soil analysis. U.S. Dept. Agric., Bur. Soils, Bull. 24. 1904. p. 33.

The use of mechanical analysis as a basis for determining the moisture retentiveness of a soil is further complicated by the fact that soils having a high clay content will show great differences in the amount of colloidal material, which greatly affects the moisture retentiveness. Furthermore, the particles constituting a given group may lie much nearer one limit of the group than the other, so that a given group does not always have the same properties. We are then led to conclude that the particles constituting a given group in the mechanical analysis do not always have the same moisture retentiveness per unit mass, or that their specific retentivity when measured alone is modified to some extent by admixture with particles from other groups.

BRIGGS and MCLANE,[20] using the method of least squares, have established a relationship between the mechanical composition and the moisture equivalent, based upon data covering 104 soil types. The resulting probable error of the coefficients in the relationship established is ±1.7 per cent.[21] In attempting the correlation of the mechanical composition with the non-available moisture, we have used the same *relative* values for the sand, silt, and clay coefficients that were obtained by BRIGGS and MCLANE in their moisture equivalent correlation. The actual values of the coefficients were adjusted to give the best calculated values for the wilting coefficient, but the same proportion among the coefficients was maintained. The formula used was as follows:

0.01 sands+0.12 silt+0.57 clay=wilting coefficient.

In this formula the "sands" refer to the percentage of particles ranging from 2 to 0.05 mm. in diameter, the "silt" to particles from 0.05 to 0.005 mm. in diameter, and the "clay" to particles smaller than 0.005 mm. in diameter. In the accompanying table[22] (table V) is given the mechanical composition of each of the soil types, the computed value of the wilting coefficient as determined by the above formula, the observed value of the wilting coefficient,

[20] BRIGGS, L. J., and MCLANE, J. W., *l.c.*, 18.

[21] This value should not be confused with the probable error of a single determination, as given by BRIGGS and MCLANE.

[22] We are indebted to the Bureau of Soils for the mechanical analysis. No mechanical analyses were available for samples nos. 6 and 14.

and the residuals or the difference between the observed and the computed values.

TABLE V

COMPARISON OF THE OBSERVED WILTING COEFFICIENT WITH THAT FOUND BY COMPUTATION FROM THE MECHANICAL ANALYSIS

No.	Soil type	Coarse sand mm. 2—0.25 percentage	Fine sand mm. 0.25—0.05 percentage	Silt mm. 0.05—0.005 percentage	Clay mm. 0.005—0 percentage	Wilting coefficient		Residuals	Ratio of obsvd. to comp.
						Computed percentage	Observed percentage		
7....	Coarse sand	60.4	37.1	0.8	1.6	1.8	0.9	+0.9	0.50
2....	Fine sand	28.2	64.4	4.7	3.9	3.1	2.6	+0.5	0.84
8....	Fine sand	35.4	55.1	4.8	4.5	3.6	3.3	+0.3	0.92
9....	Fine sand	29.9	56.7	5.0	8.2	3.8	3.6	+0.2	0.95
3....	Sandy loam	33.1	50.0	8.6	7.5	4.9	4.8	+0.1	0.98
4....	Fine sandy loam	2.8	59.8	30.2	6.9	10.3	9.7	+0.7	0.94
12....	Loam	3.4	55.5	21.8	19.1	9.5	10.3	−0.8	1.08
A.....	Sandy loam	32.4	28.8	26.7	11.8	9.9	9.9	0.0	1.00
B.....	Fine sandy loam	15.8	42.4	28.7	12.9	10.7	10.8	−0.1	1.01
C.....	Fine sandy loam	19.2	35.6	30.6	14.7	11.4	11.6	−0.2	1.02
5....	Loam	2.0	48.8	37.7	12.3	13.5	13.9	−0.4	1.03
D	Loam	3.6	35.2	41.4	14.4	14.6	15.2	−0.6	1.04
14....	Clay loam	5.1	27.0	35.2	32.5	14.5	16.2	−1.7	1.12
E.....	Clay loam	3.2	43.7	45.1	17.1	16.0	16.5	−0.5	1.03
6....	Clay loam	4.4	20.5	52.6	22.0	16.6	16.3	+0.3	0.98

The ratio of the observed to the computed value of the wilting coefficient is also given in the last column of the table in order to provide a basis of comparison as regards accuracy with the other physical measurements. The mean ratio[23] is 1.00, with a probable error of ±0.025. This large probable error is due mainly to soil no. 1, which has a departure no greater than some of the other soils, but which on account of its very small wilting coefficient gives a ratio which is widely divergent from the rest of the series. The formula for computing the wilting coefficient, when affected with its probable error, then becomes:

$$\frac{0.01 \text{ sands} + 0.12 \text{ silt} + 0.57 \text{ clay}}{1 \pm 0.025} = \text{wilting coefficient.}$$

[23] In determining the values of the sand, silt, and clay coefficients so as to give a mean ratio equal to unity, soil no. 1 was disregarded, since a better general agreement was obtained in this way. This is virtually what would have happened if the method of least squares had been applied to the experimental data. In all calculations of probable error, however, this soil has been included with the rest.

COMPARISON OF THE ACCURACY OF THE INDIRECT METHODS FOR DETERMINING THE WILTING COEFFICIENT

Since the numerical value of the ratio used in calculating the wilting coefficient by indirect methods varies considerably according to the method employed, it is necessary for purposes of comparison to express the probable error in each case as a percentage of the ratio which it affects. This comparison is given in the accompanying table (table VI).

TABLE VI

SHOWING THE COMPARATIVE ACCURACY OF THE RATIOS USED IN THE INDIRECT METHODS FOR DETERMINING THE WILTING COEFFICIENT

METHOD	RATIO	PROBABLE ERROR OF MEAN RATIO	
		Absolute value	Percentage of ratio
Moisture equivalent.....	1.84	±0.013	±0.7
Hygroscopic coefficient.....	0.68	±0.012	±1.8
Moisture holding capacity ..	2.90	±0.06	±2.1
Mechanical analysis	1.00	±0.025	±2.5

The probable error of the mean ratio shows the degree of uncertainty that is attached to the value given for the ratio. That is to say, if the moisture equivalent series were repeated, the chances are even that the mean ratio would fall between 1.827 and 1.853. In other words, in a soil having an observed moisture equivalent of 18.4 per cent, the chances are even that in so far as the accuracy of the ratio is concerned the wilting coefficient lies between 9.93 and 10.07 per cent. This corresponds to an uncertainty of ±0.7 per cent in the value of the wilting coefficient calculated by means of the ratio 1.84, as shown in the last column of the table.

The last column of the table shows the probable error of the mean ratio expressed as a percentage of the ratio itself. This affords at once a means of comparing the accuracy of the different ratios. It will be seen that the probable error arising from the uncertainty of the ratio in calculating the wilting coefficient by the moisture equivalent method is about 0.7 per cent; by the hygroscopic coefficient method 1.8 per cent, or over twice as great; by the moisture-holding capacity method 2.1 per cent, or three times as great; and by the mechanical analysis method 2.5 per cent, or nearly four times as great.

It should be recognized clearly that the formulae which have been deduced will not necessarily give the correct calculated value of the wilting coefficient within the limits of the probable error of the ratio. The uncertainty regarding the value of the observed quantity (moisture equivalent, hygroscopic coefficient, etc.) enters into the calculation of the wilting coefficient for any particular soil, in addition to the uncertainty of the ratio. According to the formulae, a linear relation exists between the observed quantity and the wilting coefficient in each case, and the observed departures are attributed to accidental experimental errors. If this is true, then the probable error of the calculated wilting coefficient for a given soil can be made to approach the probable error of the ratio as a limit simply by increasing the accuracy and number of the determinations of the observed quantity.

The probable error of a single determination of the wilting coefficients in our experiments is given below for each method, expressed in per cent of the wilting coefficient.

Moisture equivalent method, ± 2.9 per cent
Hygroscopic coefficient method, ± 7.1 per cent
Moisture holding capacity method, ± 8.3 per cent
Mechanical analysis method, ± 10.0 per cent

These errors are not to be applied to any other determinations, since they represent simply the degree of accuracy attained in our particular experiments. If the number of physical measurements made upon each soil had been increased, the error would have been reduced.

FORMULAE SHOWING RELATIONSHIPS BETWEEN PHYSIOLOGICAL AND PHYSICAL MEASUREMENTS OF MOISTURE RETENTIVITY

For convenience in reference, the formulae for determining the wilting coefficient of a given soil by indirect methods are here presented in collected form, together with the probable error.

$$\text{Wilting coefficient} = \frac{\text{moisture equivalent}}{1.84(1 \pm 0.007)}$$

$$\text{Wilting coefficient} = \frac{\text{hygroscopic coefficient}}{0.68(1 \pm 0.018)}$$

$$\text{Wilting coefficient} = \frac{\text{moisture holding capacity} - 21}{2.90(1 \pm 0.021)}$$

$$\text{Wilting coefficient} = \frac{0.01\ \text{sands} + 0.12\ \text{silt} + 0.57\ \text{clay}}{1 \pm 0.025}$$

SUBSIDIARY FORMULAE

We have also included the subsidiary formulae which follow as the result of the interrelationships established. The probable error has been omitted, since its determination from the formulae would always include the experimental errors of the wilting coefficient determination, due to the fact that the physical measurements are not directly compared.

For the determination of moisture equivalent[24]

Moisture equivalent = wilting coefficient × 1.84
Moisture equivalent = hygroscopic coefficient × 2.71
Moisture equivalent = (moisture holding capacity − 21) × 0.635
Moisture equivalent = 0.02 sand + 0.22 silt + 1.05 clay

For the determination of the hygroscopic coefficient

Hygroscopic coefficient = wilting coefficient × 0.68
Hygroscopic coefficient = moisture equivalent × 0.37
Hygroscopic coefficient = (moisture holding capacity − 21) × 0.234
Hygroscopic coefficient = 0.007 sand + 0.082 silt + 0.39 clay

For the determination of the moisture holding capacity

Moisture holding capacity = (wilting coefficient × 2.9) + 21
Moisture holding capacity = (moisture equivalent × 1.57) + 21
Moisture holding capacity = (hygroscopic coefficient × 4.26) + 21
Moisture holding capacity = (0.03 sand + 0.35 silt + 1.65 clay) + 21

These formulae establish for the first time a relationship between the various physical and physiological measurements of moisture retentivity, and while the coefficients may be modified as a result of further investigation, it is believed that the equations will prove of practical value in the study of the relationship of the plant to soil moisture, both in the field and laboratory.

For the determinations of the maximum available moisture

The maximum moisture available for growth in any soil is represented by the difference between the moisture holding capacity and the wilting coefficient. It is possible, therefore, to express the *maximum* amount of available moisture that a soil is capable of holding in terms of the relationships given above. It should be recalled that the moisture-holding capacity determinations, upon

[24] These equations refer to moisture equivalent determinations made with a centrifugal force equal to 1000 grams and should not be confused with the equation given by BRIGGS and MCLANE (*l.c.*) in which a force of 3000 grams was employed.

which the relationships are based, were made with a soil column 1 cm. in height. The amount therefore is far in excess of that found in drained soils under field conditions. The relationships are expressed in the following formulae:

Maximum available moisture = (wilting coefficient $\times 1.9$) $+21$
Maximum available moisture = moisture equivalent $+21$
Maximum available moisture = (hygroscopic coefficient $\times 2.8$) $+21$
Maximum available moisture = (0.02 sand $+0.23$ silt $+1.08$ clay) $+21$
Maximum available moisture = (moisture holding capacity $\times 0.65$) $+7$

The formulae show that difference in the maximum amount of available moisture that two soils are capable of holding is equal to the difference in their moisture equivalents; to 1.9 times the difference of their wilting coefficients; and to 2.8 times the difference of their hygroscopic coefficients.

Summary

An investigation was made to determine whether the wilting coefficient of a soil can be computed from physical measurements of its moisture retentivity. A comparison of the wilting coefficient is made with the moisture equivalent, the hygroscopic coefficient, the moisture-holding capacity, and the mechanical analysis, for a series of soils ranging from sand to clay. From this comparison, a series of linear relationships is established, as expressed in the following equations, which form a means of computing the wilting coefficient when direct determinations are not feasible.

$$\text{Wilting coefficient} = \frac{\text{moisture equivalent}}{1.84\ (1 \pm 0.007)}$$

$$\text{Wilting coefficient} = \frac{\text{hygroscopic coefficient}}{0.68(1 \pm 0.018)}$$

$$\text{Wilting coefficient} = \frac{\text{moisture holding capacity} - 21}{2.90(1 \pm 0.021)}$$

$$\text{Wilting coefficient} = \frac{0.01\ \text{sand} + 0.12\ \text{silt} + 0.57\ \text{clay}}{1 + 0.025}$$

The second term of the quantity within the brackets shows the probable error of the relationship in each case, and constitutes a measure of the relative accuracy of the different methods.

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AN ISOLATED PRAIRIE GROVE AND ITS PHYTOGEOGRAPHICAL SIGNIFICANCE[1]

HENRY ALLAN GLEASON

(WITH TWO FIGURES)

Probably less study has been given in recent times to the relation of prairie and forest than to any other general phytogeographical problem in the central states. Some of the large number of questions still awaiting satisfactory solution were briefly stated in a former paper,[2] and in the following pages some evidence bearing on one of them is given and some conclusions of a more general nature are drawn. The present paper is not so much a description of modern conditions as an attempt to explain by existing distribution certain historical features of the relation of forest and prairie in central Illinois. It is probable that the conclusions drawn from the local area apply equally well to many other portions of the eastern extension of the Prairie Province.

Early histories and maps show that the prairies of central Illinois were not continuous, but occupied chiefly the higher ground between the drainage systems. The latter were bordered in their lower courses by forests, which occupied the floodplain and bluffs and extended out a short distance on the uplands. The sources of the streams were usually in the prairie, and their margins were occupied by prairie vegetation for the first few miles. Scattered about on the prairie were a few isolated groves, far removed from the larger bodies of forest along the water courses. These groves were important to the Indians and early settlers as landmarks and camping grounds, and at a later period formed centers from which the settlement of the prairie proceeded. Bur Oak Grove is an example of such an isolated area of forest. It is situated in the east-central part of Champaign County, on the east side of the

[1] Contribution no. 123 from the Botanical Laboratory of the University of Michigan.

[2] Some unsolved problems of the prairies. Bull. Torr. Bot. Club **36**: 265–271. 1909.

Chicago and Eastern Illinois Railway, not far from the village of Royal. There were several other isolated groves in the county, most of which have been entirely destroyed by cultivation. Of these, Bur Oak Grove is the largest and the most significant phytogeographically. The remaining forest areas of the county are along the Sangamon and Kaskaskia rivers, and Salt Fork of the Vermillion River. The last two rise in the county, and the upper five to ten miles of their course is in the prairie.

The present length of Bur Oak Grove is about three miles from northeast to southwest, and its width about one mile. It is certain that it was originally somewhat longer, and it probably had a greater average width. Its outline is and has always been very irregular. In recent years cultivation has broken it up into many small detached portions. There is no easily accessible map showing the location of the grove in detail. The Urbana sheet of the Topographic Survey just misses the grove on the west. Just southwest of Bur Oak Grove, however, are two or three other detached groves of similar topography which appear on the map. These areas are indicated in green near Glover station. The peculiar topography associated with these groves is scarcely shown, even on a map with contour intervals at ten feet.

The most striking physical feature of the grove is its peculiar surface topography. Surrounded on all sides by level prairie country, it is sharply and conspicuously distinguished by its irregular surface, which consists of alternating elevations and depressions. The elevations are of about the same height, and the intervening depressions are also of a very uniform depth. The width of the depressions varies from a hundred feet to a quarter of a mile; their length from a few hundred feet to half a mile, or perhaps more; and their depth is usually about ten feet. Their shape accordingly varies from almost circular to linear, and those of the latter shape frequently resemble abandoned channels of some water course. They lie in every conceivable position, and may branch or anastomose in any way. As a result of the general irregularity, the intervening elevated ground may consist of circular islands, extended surfaces, or long and narrow, straight, curved, or branching ridges. For convenience, they are here always

referred to as ridges, irrespective of their shape, while the depressions are called sloughs, after the general usage of the region. The slope from ridge to slough is always gentle, never exceeding and seldom reaching 10°. No attempt will be made to explain the origin of this peculiar topography, except to suggest that it may be in some way connected with or caused by the glacier which deposited the conspicuous moraine a few miles farther north.

These sloughs received all the surface drainage from the ridges, and were originally filled through most of the year with standing water. During the spring rains they overflowed at the lowest point in their margins into neighboring sloughs, and in this way the whole area was converted into a network of ponds. During the summer the water was lost by underground drainage and evaporation, until by October some of the sloughs were entirely dry.

These conditions have greatly restricted agriculture, and it is to them that the grove owes its preservation. With the increasing value of land, tile has been laid, ditches dug, and most of the sloughs reclaimed. In them the soil is black and deep and is generally planted to corn. Others are left in pasture, although they support a better growth of weeds than of grass. A few are so deep that they cannot be profitably drained, and are still occupied by permanent ponds. Probably half a dozen of these ponds are left, and they now constitute the only natural bodies of permanent standing water in the county. Although the soil on the ridges is not so black or so deep as on the surrounding prairies, a part of the forest which covered them has been cleared, and the staple crops are grown. The rest of the forest is used for permanent pasture.

The forest cover of the ridges shows a considerable variation in specific composition from south to north. Near the south end the forest is open, the trees are comparatively small, and there is scarcely any deposit of leaf mold (fig 1). The prevailing trees are *Quercus imbricaria*, *Q. velutina*, *Carya ovata*, *C. cordiformis*, with occasional trees of *Juglans nigra*. The actual proportion of these species varies widely. *Quercus imbricaria* is usually most abundant, but there are some small areas in which *Carya ovata* is dominant. The trees now seldom exceed a foot in diameter, but the present forest is almost

entirely second growth. Old stumps may be seen which are two feet or more in diameter, and a few veteran trees are still standing. The forest is open enough to permit the growth of blue grass, and the continual pasturage has resulted in the destruction of nearly all the native herbaceous species. The chief native plants remaining are *Muhlenbergia Schreberi*, *Geum canadense*, *Sanicula canadensis*, and *Veronica virginica*, and occasionally a small thicket of *Corylus americana*. *Verbascum Thapsus* and some other introduced weeds are frequent. At the margin of the forest there are

FIG. 1.—Forest at south end of the grove; *Quercus imbricaria* is here the dominant tree.—Photograph by ARTHUR G. VESTAL.

in some places small thickets of *Pyrus coronaria*, *Crataegus* sp., *Prunus americana*, and *Viburnum prunifolium*.

Near the middle of the grove, from south to north, several other species of trees are common. Most important among these in size and number is the bur oak, *Quercus macrocarpa*, which gave the grove its name. A few large trees, three to four feet in diameter, serve to give some idea of the dimensions of the original stand. There are also numerous trees of *Juglans nigra*, *Ulmus fulva*, *Celtis occidentalis*, *Prunus serotina*, and *Gleditsia triacanthos*. The four species of the south end of the grove are still present, although naturally relatively less abundant. Near the margin of this portion

of the forest, and in the more open places within it, avevectent shrubs are abundant. The commoner ones are *Smilax hispida*, *Menispermum canadense*, *Crataegus Crus-galli*, *Crataegus* sp., *Evonymus atropurpureus*, *Celastrus scandens*, *Psedera quinquefolia*, *Vitis vulpina*, *Zanthoxylum americanum*, *Sambucus canadensis*, and *Viburnum prunifolium*. Where the forest is too dense to permit the growth of blue grass, many of the original herbaceous species still persist. Among them the following were listed: *Dioscorea villosa*, *Parietaria pennsylvanica*, *Polygonum virginianum*, *Phytolacca decandra*, *Silene stellata*, *Anemone virginiana*, *Aquilegia canadensis*, *Heuchera hispida*, *Agrimonia mollis*, *Rosa setigera*, *Lespedeza frutescens*, *Amphicarpa monoica*, *Polygala Senega* var. *latifolia*, *Viola* sp., *Sanicula canadensis*, *Seymeria macrophylla*, *Triosteum perfoliatum*, *Campanula americana*, *Helianthus strumosus*, *Verbesina helianthoides*, *Aster Drummondii*, *Lactuca villosa*.

In the northernmost part of the grove the four trees of the southern end still persist, but are much less abundant than other species. *Quercus macrocarpa*, *Juglans nigra*, *Celtis occidentalis*, and *Ulmus fulva* are common; *Gleditsia triacanthos* grows 60–80 feet high; there are a few trees of *Prunus serotina*, *Ulmus americana*, and *Populus grandidentata*, and, most notable from an ecological viewpoint, *Quercus rubra* and *Tilia americana* appear. At the northeast corner of the grove *Quercus rubra* is the dominant species, with the largest living trees about three feet in diameter. In this part of the grove there is a conspicuous deposit of leaf mold on the ground, and the forest cover produces a denser shade. As a result, the herbaceous vegetation is decidedly mesophytic and includes many species which are typically members of the climax forest association. Among these are *Arisaema triphyllum*, *Allium tricoccum*, *Trillium recurvatum*, *Smilax ecirrhata*, *Pilea pumila*, *Ranunculus abortivus*, *Podophyllum peltatum*, *Impatiens pallida*, *I. biflora*, *Circaea lutetiana*, *Cryptotaenia canadensis*, *Phlox divaricata*, *Pentstemon laevigatus* var. *Digitalis*, *Phryma Leptostachya*, *Galium concinnum*, and *Eupatorium urticaefolium*. Avevectent shrubs are not so common as in the middle portion of the forest, and blue grass grows only in partial clearings.

Direct observation shows at once that the forest is always con-

fined to the ridges, and measurement with a Locke level or alidade not only confirms this idea, but shows that the lower and outer margin of the forest follows a definite contour line, so that the forest margins on all sides of a slough lie at exactly the same level. This contour line is approximately two feet above the maximum level of standing water in the slough. The forest margins on opposite sides of a ridge will be at the same level if the sloughs are connected, but otherwise they may differ slightly in elevation. Within the forest, the various species of trees, with one exception, show no relation to the elevation, but are equally abundant on the sides and top of the ridges. The exception is formed by *Gleditsia triacanthos*, which regularly chooses the lower outer margin, nearest the sloughs and in the wettest soil. This feature has been observed also in other isolated groves in the county. The shrubs, if present at all, seem to prefer the margin of the forest, but in this case the controlling factor is probably light instead of water.

Some very definite and sharply marked zones of vegetation occur between the forest and the center of the pastured sloughs. The first is a zone of blue grass which extends out beyond the forest margin to a distance depending on the steepness of the slope, and down to the former level of maximum high water in the slough. Because of the continual pasturage it contains few secondary species. The second zone is composed of a very dense and rank growth of *Ambrosia artemisiifolia*, with scattered plants of *Vernonia fasciculata*, *Eupatorium serotinum*, *Bidens cernua*, *B. aristosa*, *Polygonum acre*, and *Verbena hastata*. It is probable that the dominance of *Ambrosia*, and the relative infrequency of other species, is caused by pasturing, in which certain species are selected for food, and others with rank smell or taste are avoided by the cattle and horses. This idea is substantiated by the different composition of the same zone around a slough in an unpastured field. In this tangle of weeds may be found a few scattered plants of some typical swamp hydrophytes, such as *Iris versicolor*, *Mimulus ringens*, *Scirpus fluviatilis*, and *Penthorum sedoides*. These are naturally most abundant in the deepest part of the slough, but show no present relation to contour lines (fig. 2).

Around those sloughs which contain permanent ponds a better

idea of the zonation may be gained. In such places the second zone contains some *Ambrosia*, but the dominant species are various grasses and sedges, especially *Leersia oryzoides* and *Glyceria nervata*. *Bidens aristosa* is common, and there are numerous scattered plants of the species mentioned before. Within and below this zone is a third, in which the dominant plants are again grasses and sedges, and in which *Iris versicolor*, *Mimulus ringens*, *Penthorum sedoides*, *Lippia lanceolata*, *Asclepias incarnata*, *Lobelia siphilitica*, and other

FIG. 2.—Relation of vegetation to topography; the drained slough in the foreground, with prominent clusters of *Iris*, is contrasted with the forest-covered ridge at the left.—Photograph by ARTHUR G. VESTAL.

characteristic hydrophytes are abundant. A fourth zone at the margin of the pond is characterized by *Scirpus validus*, *Salix longifolia*, *Eragrostis hypnoides*, *Eleocharis obtusa*, *E. acicularis*, and *Ludvigia palustris*.

It has not been many years since all the sloughs contained permanent standing water, which has been removed by tile drains or open ditches. By this the fourth, or innermost, zone has been destroyed completely, the third has been limited to a few scattered relics, and the second has extended in and occupied most or all of the space. Then pasturage has destroyed the dominant grasses and sedges and caused the invasion of weedy species.

Every plant listed as living in the sloughs is by preference a prairie species. Throughout the series not one typical plant of the forest has been seen. Such common and characteristic plants of floodplain swamps and oxbows as *Hibiscus militaris*, *Cephalanthus occidentalis*, and *Ambrosia trifida* are entirely absent. The oldest settlers say that there never were either white or yellow water lilies. On the contrary, they state that the margins of the sloughs were occupied by "slough grass" (*Spartina Michauxiana*) tall enough to hide a man on horseback. So it is obvious that these were prairie sloughs rather than forest swamps, and that the vegetation must have been entirely distinct from and independent of the forest vegetation of the ridges. A reconstruction of the whole grove would present a series of prairie sloughs, with grassy vegetation, alternating with the series of forested ridges. An interpretation of the phytogeographical significance of this condition will now follow.

The forest evidently indicates three stages in a successional series, beginning with the oaks and hickories at the south, passing through the bur oak stage at the center, and ending with the red oak stage near the north end. This succession is the usual one for central Illinois, and is caused, at least in part, by the gradual accumulation of humus and decrease in light. There are many other places in the state where the same series may be observed under different ecological circumstances. It is especially typical of the succession of forests on uplands along a stream, and is met with in traversing such a forest at right angles to the course of the stream. The presence of a few trees of basswood at the extreme north end may be construed to indicate the approaching development of the hard maple-basswood type of forest, the highest type found in central Illinois. Along stream courses this normally follows the red oak stage, and is located accordingly nearer the stream. The chief difference between the forests of a river system and Bur Oak Grove lies not in their structure, but in the fact that the former are connected with a general forest system extending down the river to an indefinite distance, while in the latter the grove is entirely isolated from other bodies of forest. The origin of the forests of a river system can be explained by the gradual and continuous

immigration of plants along a river highway. In the isolated grove it must be explained by a connection, no longer existent, with an older forest source, or by the sporadic development of the forest following a discontinuous migration across the prairie.

Considering the second alternative, it might be possible for the various successional stages to develop centrifugally about a small forest center, the first stage occupying an outer ring, while the following ones appeared toward the middle. This does not seem possible here, because the arrangement is so obviously unilateral, with the later stages in the succession progressively farther toward the northeast, while there is no obvious difference in the environment between the two ends of the grove, which might lead to the readier development of the red oak stage at one end. Also, in every other forest examined in central Illinois, in which oaks are the dominant trees, it has been possible to show a definite connection with some other body of forest, from which continuous migration might have taken place. In other words, oaks, with their heavy immobile seeds, do not seem able to cross tracts of prairie to a more favorable habitat, but must migrate in an uninterrupted path. There are isolated groves in Champaign County, whose structure suggests that they are the result of a discontinuous migration, but no oaks occur in them.

Considering now the first alternative, the development of Bur Oak Grove through immigration along the small streams of the vicinity is precluded for several reasons. First, their valleys are too shallow to afford the necessary physiographic diversity which always accompanies a mesophytic type of forest in central Illinois. Secondly, they all flow to the south, while in Bur Oak Grove the more mature forest type is at the north. Thirdly, they would have served as well or better for the immigration of hydrophytes than for upland species, while, as has been shown, the hydrophytic vegetation of the grove consists entirely of prairie species. The arrangement of species in the grove is exactly similar to the unilateral arrangement paralleling water courses in central Illinois. The whole grove has the appearance, and conveys the impression, of being the margin, now the only part remaining, of some extensive body of forest immigrating from the northeast, the location

of the more advanced stages, toward the southwest, the present location of the pioneer black oak and shingle oak. Of all the possibilities, development of the grove by continuous immigration from the northeast seems the only plausible explanation, and is accepted as the correct conclusion.

This idea postulates the existence in the past of a large tract of forest farther to the northeast, from which immigration into the grove took place. A few miles beyond the grove a moraine extends from northwest to southeast, perpendicular to the general direction of the forest migration, and beyond the moraine and parallel to it is the Vermillion River, bordered with a narrow belt of forest. The original source of Bur Oak Grove must be looked for at the river or along the moraine.

Several reasons lead to the belief that the moraine was the site of the ancient forest from which Bur Oak Grove was populated. In the first place, the scanty forests along the river are entirely incommensurate in size, and the distance is too great. Secondly, moraines in northeastern Illinois and parts of central Illinois are regularly forested, and other moraines in Champaign County have even now small groves upon them. Most important of all, various moraines in central Illinois have upon them forest relics which point indubitably toward a former forest covering. Thickets of hazel, an immobile forest plant not seriously injured by forest fires, are known from several places. On the moraine north of Bur Oak Grove, *Erythronium albidum*, *Trillium recurvatum*, and *Claytonia virginica* occur. These forest mesophytes produce seed in this region so seldom and propagate by vegetative means so regularly, that they cannot be considered recent invaders from the forest upon the prairie. They die to the ground in the summer, before the season of prairie fires, and their persistence on the prairie is probably due to this habit, together with their ability to withstand exposure to the full sunlight. Because of these three reasons, it seems probable that the moraine was originally covered with a forest of some luxuriance, and that from it as a center invasion of the surrounding prairies took place. Other moraines must have been similarly forested, so that in some prehistoric time a vastly larger proportion of the state was covered with forest than at pres-

ent. The entire absence of forest relics over most of the prairie makes it extremely improbable that the entire surface of the county was ever forested. The level till plains between the stream systems and the moraines were probably prairie even at the time of greatest forest advance. The immigration of the forest was restricted to the two lines of greatest physiographic diversity, the stream valleys and the moraines.

We must now account for the removal of this large body of forest from the moraine, and for the persistence of the small remainder in a few outlying tracts like the one at Bur Oak Grove. Examination of the conditions in the grove will suggest the reason, which is substantiated by other observations elsewhere in the county.

Along the western margin of the grove some of the ridges are still forested, while others are under cultivation. Examination of the vegetation along the roadsides on the cultivated ridges shows on some of them such typically forest plants as *Aster Drummondii*, *Silene stellata*, *Hedeoma pulegioides*, and others. It is evident from the flora that these ridges were originally forested also. On some other ridges these species are entirely absent, and the roadside vegetation consists of typically prairie species, as *Andropogon furcatus*, *Sorghastrum nutans*, *Panicum Scribnerianum*, *Silphium integrifolium*, *Petalostemum violaceum*, and *Parthenium integrifolium*. Evidently these ridges were originally prairie. By this method of observation of the relic plants, the exact boundaries of the grove can be determined. In this way it becomes evident that, in every case, those ridges which are or were forested are protected on the west by a conspicuous slough, while the prairie ridges extend west without interruption out upon the open prairie. Since the forested part of the grove is exclusively on the ridges, it is clear that the whole forest was protected on the west side by a series of sloughs. The prevailing winds are also from the west, and prairie fires driven to the eastward by a west wind were unable to cross the slough into the forest. It may be concluded, accordingly, that prairie fires were the chief and probably the only agent in the removal of the forest from the moraines and other places where it was not properly protected by a water barrier. The grove

at Bur Oak was benefited by a peculiar and unusual topography, and was virtually the only portion of an extensive forest system to be spared.

The origin of the prairie as a type of vegetation cannot, however, be referred to prairie fires as a cause, as was frequently supposed by early authors and occasionally even in recent years. A prairie fire presupposes a prairie, and in prairie fires we have merely one factor which has been of assistance in the maintenance or extension of the prairie in its struggle against forest invasion. In the last half century, since the cessation of prairie fires, the forests have again begun an advance into the prairie, but, as is well known, their route is chiefly up the streams, and the migration is limited to a comparatively small number of mobile species. Because of increasing cultivation, this migration is very irregular and can never lead to any serious modification in the vegetation of the region.

In conclusion, the conditions in Bur Oak Grove serve to indicate the last three periods in the vegetational history of the state:

1. Period of forest advance, leading to a great development of forests in areas of physiographic diversity.

2. Period of prairie fires, following the advent of man and leading to the restriction of the forest to protected areas and the corresponding extension of the prairie.

3. Period of civilization and the virtual cessation of the struggle between forest and prairie.

UNIVERSITY OF MICHIGAN

SOME FEATURES IN THE ANATOMY OF THE SAPINDALES[1]

RUTH HOLDEN

(WITH PLATES II AND III)

In studying the phylogeny of plants, there are certain general principles upon which all conclusions are based. One of these deals with the retention of ancestral characteristics. A striking example of this is afforded by the anatomy of the cycads. The vegetative stem of these forms always has exclusively centrifugal metaxylem, but in the leaf petiole, the metaxylem is predominately centripetal, with only a slight development in a centrifugal direction. Centripetal wood structure is, of course, the more primitive, and its appearance in the leaf petiole of the Cycadales serves to relate them to their extinct Cycadofilicean ancestors, where centripetal wood was present in the stem. Similar bundles with centripetal wood are present also in the reproductive axes of certain Cycadales.[2]

Another well known seat of primitive conditions is the root, good examples of which are furnished by the Abietineae. The first and older subtribe, the Pineae, is characterized by the invariable presence of resin canals in the normal wood of both root and stem, while in the more modern subtribe, the Abietae, resin canals are generally absent in the normal wood of the stem. Resin canals do occur, in all four genera of the Abietae, in the center of the primary wood of the root.[3]

Recent investigations have shown that ancestral conditions may be recalled as a result of wounding. For example, these resin canals, present in the roots of the Abietae, are present invariably

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 42.

[2] SCOTT, D. H., The anatomical characters presented by the peduncle of Cycadaceae. Ann. Botany 11:399–419. *pls. 20, 21.* 1897.

[3] JEFFREY, E. C., The comparative anatomy and phylogeny of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. 6:1–37. *pls. 1–7.* 1904.

in the wood formed immediately after injury. Anatomical evidence thus shows that there are present in the leaf, petiole, root, and wounded tissue of gymnosperms, structures quite unlike those normally occurring in the stem; and paleobotanical evidence shows that these are primitive features, retained in certain restricted localities long after they have disappeared elsewhere. Instance after instance could be cited where these two lines of evidence, anatomical and paleobotanical, reinforce each other in the gymnosperms. In the angiosperms, however, no such checking up is possible as yet, because of the comparative scantiness of fossil material. Here the anatomical principles worked out from a study of gymnosperms have to be relied on exclusively in tracing their phylogeny.

Another principle of comparative anatomy is that simple conditions are not necessarily to be interpreted as primitive. This is well recognized by zöologists, who regard tunicates as vertebrates which, in losing almost entirely their vertebrate characteristics, have reverted to a simpler ancestral organization, and as degenerate rather than primitive. Or, on the botanical side, *Abies* has as simple normal wood as any known; there are only two types of elements present, tracheids and parenchyma, transverse and longitudinal. In the roots of all species, however, there are specialized resin canals, surrounded by parenchymatous epithelial tissue; these are present also in the reproductive axes of certain species. Another complication is present in the wounded root of at least one species,[4] where above and below the parenchymatous ray cells there are rows of tracheidal cells, forming ray tracheids like those of *Pinus*. Applying the principles of comparative anatomy, it is evident that *Abies* is descended from forms which had both resin canals and ray tracheids, and its simplicity of wood structure is not primitive, but a result of degeneracy.

It is the purpose of this paper to present the conditions found in certain of the Sapindales, and then to interpret them in accordance with these principles. For this purpose, four representative genera were chosen; *Aesculus*, *Acer*, *Sapindus*, and *Staphylea*.

[4] THOMPSON, W. P. The origin of ray tracheids in the Coniferae. BOT. GAZ. 50:101–116. 1910.

Fig. 1 shows a transverse section of the wood of *Aesculus Hippocastanum* L., and fig. 2 a tangential section of the same. From these it is possible to make out the main features of the wood. Woods may be grouped into three classes, depending on the distribution of parenchyma: (1) a primitive type with only terminal parenchyma on the "face of the summer wood"; (2) a more advanced type with parenchyma scattered throughout the year's growth, that is "diffuse"; and (3) the highest type with parenchyma only around the vessels, or "vasicentric." *Aesculus* belongs to the third of these groups; furthermore, its parenchyma is chiefly on the tangential wall of the vessels. The mechanical elements of the wood also exhibit a high degree of specialization, in that they are all transformed to libriform fibers, with characteristically thick walls, and narrow, obliquely elongated simple pits. The vessels are scattered throughout the year's growth, giving the "diffuse porous effect." The vessels have pits on the side walls closely crowded together, but never fused, end walls with porous perforations, and tertially spiral thickenings on their inner walls. Thus in having vasicentric parenchyma, libriform fibers, and vessels with porous perforations, *Aesculus* has the wood structures characteristic of the highest dicots, but the rays present a peculiarly simple condition. They are always of the linear, uniseriate type, like those of many of the gymnosperms.

Figs. 1 and 2 represent *Aesculus Hippocastanum*, but the wood is practically indistinguishable from that of its near relative *Aesculus glabra* Willd., as well as other species of the genus, and this description applies equally to all.

Fig. 3 represents a tangential section of *Acer saccharum* Marsh. The wood is "diffuse porous" like that of *Aesculus*, and the parenchyma is likewise vasicentric, but less abundant, and instead of being on the tangential wall, it is on the radial wall. The libriform fibers are heavier than those of *Aesculus*, especially those immediately around the vessels, which are very thick walled, while those in the intervals are larger and thinner walled. The vessels are very similar to those of *Aesculus*, having porous perforations on the end walls, densely crowded pits on the side walls, and well marked tertiary thickenings. The rays, however, are strikingly

different. These are a few of the uniseriate variety, but the majority are multiseriate.

Figs. 4 and 5 represent transverse and tangential sections of the wood of *Sapindus* sp. Like the two genera described, the wood is "diffuse porous"; the parenchyma is vasicentric and abundant. The fibers are characterized by delicate cross partitions of cellulose, constituting the so-called "septate fibers." Though some of the vessels are small, the majority are large, serving at once to separate *Sapindus* from the other members of the Sapindales. They have porous perforations and spiral thickenings; the side walls in some places have closely crowded pits, but in other places there is a decided tendency toward fusing into rows of slitlike bordered pits. The rays of *Sapindus* are multiseriate, much like those of *Acer*.

Fig. 6 represents another member of the Sapindales, *Staphylea trifolia* L. Here the wood parenchyma is vasicentric, and usually on the radial side of the vessels. The wood elements are not as specialized as in the other genera; instead of being libriform or septate fibers, they are fiber tracheids, with thinner walls and conspicuously bordered pits. The vessels have both porous and scalariform perforations; the pits on the side walls are sometimes unfused like *Acer* and *Aesculus*, but are more often united to form large slit like openings. *Staphylea* is the only one of the four genera examined in which there are no spiral markings on the inner walls of the vessels. The rays range from 1 to 10 cells wide. These broad rays cause a local "dipping in" of the annual ring, like that in *Quercus*.

Having considered the general characteristics of these four members of the Sapindales, the question arises as to which is the most primitive and which the most advanced. Disregarding the evidence furnished by the ray, *Staphylea*, with its scalariform perforations and fiber tracheids, seem to be the lowest; but taking the ray structure into consideration, *Aesculus* seems to be the lowest. Thus the question narrows down to which is the more primitive for the Sapindales, uniseriate or multiseriate rays.

In this connection it is interesting to note the work of EAMES of this laboratory on the genus *Quercus*.[5] He found the rays of

[5] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**: 161–167. *pls. 8, 9.* 1910.

Quercus to be of two sorts, linear or uniseriate, and broad or compound. In investigating the relative primitiveness of these two types, he examined a fossil oak from the Miocene. Here he found the same two sorts of ray, uniseriate and broad, but the broad rays, instead of being homogeneous masses of parenchyma, were composed of smaller rays, separated from each other by fibers, or by fibers and wood parenchyma. This condition lead to the suspicion that broad rays of living oaks might be derived from the aggregation and fusion of small rays. Accordingly, he examined seedlings of a number of oaks, and found such to be the case. Seedlings of black oaks show, near the pith, a ray structure like that of the miocene oak, with a gradual, progressive fusion until a single, homogeneous, compound ray is formed. Seedlings of white oaks show a still more primitive condition. In some, for the first 15 or 20 years, only uniseriate rays appear, which generally fuse into compound rays. Thus both anatomical and paleobotanical evidence point to the conclusion that for *Quercus* uniseriate rays are primitive, and that the large rays are formed by a process of fusion.

This conclusion is further strengthened by a consideration of conditions found in wounded oaks. BAILEY[6] of this laboratory investigated a number of species of this genus, and found that in every case, after a severe wound, a broad ray breaks up into a number of uniseriate or small rays, a clear case of traumatic reversion.

This compounding process BAILEY has examined in a number of genera of the Betulaceae and Fagaceae, with similar results. For example, in *Alnus*[7] he finds all types, from exclusively uniseriate rays in *A. acuminata* H.B.K. to completely fused aggregate or compound rays in *A. rhombifolia* Nutt.

The uniseriate rays of *Aesculus*, therefore, are open to two interpretations; they may be primitive like those of white oak seedlings, in which case *Aesculus* has a very low type of wood structure; or they may be the result of reversion, in which case *Aesculus* is

[6] BAILEY, I. W., Reversionary characters of traumatic oak woods. BOT. GAZ. 50:374–380. *pls. 11, 12.* 1910.

[7] BAILEY, I. W., Relation of the leaf trace to the origin and development of compound rays in the dicotyledons. Ann. Botany (ined.).

descended from ancestors which had multiseriate rays like those of *Acer*, *Sapindus*, and *Staphylea*. In determining this point, one must rely on the principles of comparative anatomy worked out for the gymnosperms, and investigate the parts of a plant which are most tenacious of ancestral characteristics, namely, leaf petiole, reproductive axis, and root.

Figs. 7 and 8 represent transverse sections of the leaf petiole of *Aesculus Hippocastanum;* fig. 9 a tangential section of the same, and in all three the multiseriate type of ray is conspicuous. When a leaf petiole leaves the branch, there is no one woody cylinder, but instead, 20–30 small vascular strands. Most of these strands arrange themselves in the form of a circle, and fuse to form a siphonostele, but certain ones, perhaps 5–10, instead of taking up a peripheral position, remain in the center. These medullary bundles are at first collateral in structure, but soon the xylem begins to grow around the phloem, until they become amphivasal, forming bundles such as are found typically in monocot rhizomes. This siphonostelic condition with medullary bundles is found throughout the length of the petiole, up to the bases of the leaflets. Then the cylinder is broken again into a large number of vascular strands, which in the bases of the leaflets repeat the process carried on in the base of the petiole. Some take up a peripheral position and form a siphonostele, while one or two remain in the pith as medullary bundles. These medullary bundles, however, are always collateral, never amphivasal. The important point is that throughout the prevailing type of ray is multiseriate. This is equally true of the separate strands as they leave the main branch, of the woody tissue of the siphonostele of both petiole and leaflet, and of the medullary bundles of both petiole and leaflet. Usually the rays as they leave the pith are biseriate or triseriate; sometimes they remain so to the cambium, but usually they become reduced to a uniseriate condition. Another peculiar condition seen in tangential section is the longitudinal elongation of the ray cells.

It is one of the principles of plant anatomy that the leaf trace is tenacious of ancestral conditions, and it is interesting to note that in the case of *Aesculus* these primitive conditions are retained,

not only in the leaf trace, but also in the wood of the axis immediately around the leaf trace. Fig. 10 represents an outgoing foliar bundle; subtending it, there is a mass of ray parenchyma forming a true multiseriate ray. Often in the case of numerous small bundles going into the petiole, this mass of tissue extends all the way from one bundle to the next.

These photographs are all of *Aesculus Hippocastanum*, but the conditions of *Aesculus glabra* are essentially the same, except that under the leaf trace there is seldom as much parenchyma as here shown.

Fig. 11 is a tangential view of the wood of a root, showing an outgoing rootlet and the tissue immediately under it. The conditions are very much as in the branch, each rootlet trace being subtended by numerous multiseriate rays. Usually, however, this condition is not so pronounced in the root as in the branch.

Fig. 12 is a tangential section of a floral axis, showing the conditions immediately below an outgoing flower stalk or peduncle. The rays are characteristically biseriate, and extend sometimes a long distance below the trace. Often above the trace they are broader than below, but they never extend as far. The woody tissue is as a whole poorly developed, except at the end of each flower stalk, where it becomes much thicker. Just below the end, there are 5 or 6 traces going out simultaneously, each of which has a small number of multiseriate rays below it.

Three of the recognized primitive localities have thus been shown to have well marked multiseriate rays, and wounded wood was examined for the same structures. None were found, either because the injury was not sufficiently severe, or because the degeneracy of *Aesculus* has gone too far to be recalled traumatically.

Aesculus then presents a condition just the reverse of that found in *Quercus*. The former has uniseriate rays normally, with multiseriate rays persisting in primitive localities; the latter has compound rays normally, with uniseriate rays in primitive localities. Accordingly, multiseriate rays are primitive for the Sapindales, and *Aesculus*, instead of being the most primitive of the Sapindales, on the basis of ray structure, is really advanced, its simplicity being due to degeneracy.

Summary and conclusions

1. Investigations of the anatomy of living and fossil gymnosperms have proved certain general principles. One is that primitive structures occur in the fibrovascular bundles of the leaf petiole, the root, and the reproductive axis, and sometimes revert in wounded wood.

2. Of the Sapindales investigated, three show multiseriate rays normally: *Acer*, *Sapindus*, and *Staphylea;* the fourth, *Aesculus*, shows uniseriate rays normally, but multiseriate rays in the leaf petiole, root, and reproductive axis.

3. Applying the general principles enumerated above, it is evident that the multiseriate type of ray is primitive for the Sapindales, and that *Aesculus* is a degenerate member. Accordingly, the Sapindales belong high in any systematic arrangement of dicotyledonous woods.

In conclusion, I wish to express to Dr. E. C. JEFFREY my sincere thanks for his suggestions and advice during the course of this investigation.

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EXPLANATION OF PLATES II AND III

PLATE II

FIG. 1.—*Aesculus Hippocastanum;* transverse section of wood, showing uniseriate rays; ×80.

FIG. 2.—The same: tangential section of wood, showing similar rays; ×80.

FIG. 3.—*Acer saccharum:* tangential section of wood, showing multiseriate rays; ×80.

FIG. 4.—*Sapindus* sp.: transverse section of wood, showing multiseriate rays; ×80.

FIG. 5.—The same: tangential section of wood, showing similar rays; ×80.

FIG. 6.—*Staphylea trifolia:* tangential section of wood, showing multiseriate rays; ×80.

PLATE III

FIG. 7.—*Aesculus Hippocastanum:* transverse section of leaf petiole, showing multiseriate rays; ×180.

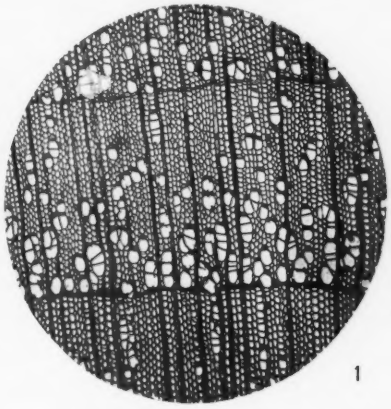
FIG. 8.—The same: transverse section of leaf petiole in another region, showing similar rays; ×180.

FIG. 9.—The same: tangential section of leaf petiole, showing similar rays; ×80.

FIG. 10.—The same: tangential section of branch, showing outgoing foliar bundle with subtending multiseriate rays; ×80.

FIG. 11.—The same: tangential section of root, showing outgoing rootlet with subtending multiseriate rays; ×80.

FIG. 12.—The same: tangential section of reproductive axis, showing multiseriate rays below outgoing flower stalk; ×80.



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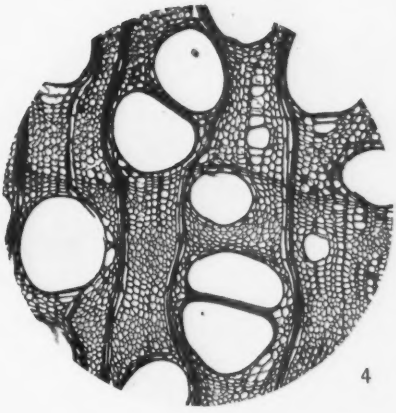

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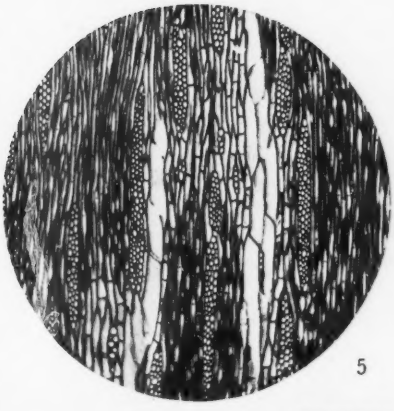

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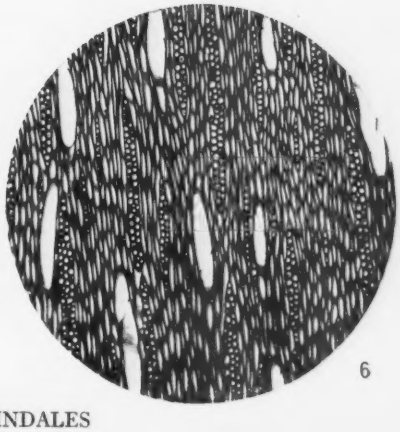

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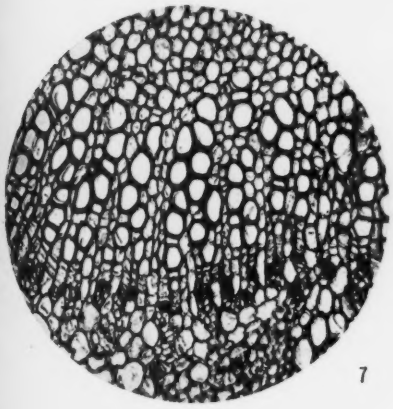
HOLDEN on SAPINDALES



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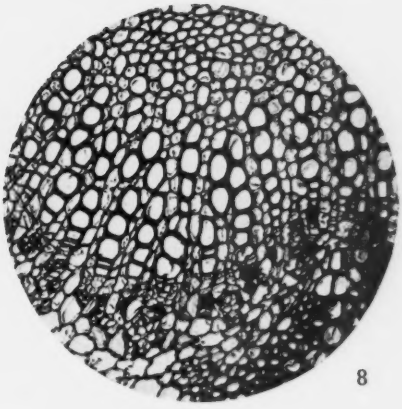

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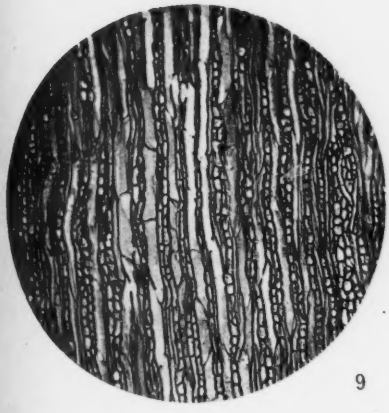

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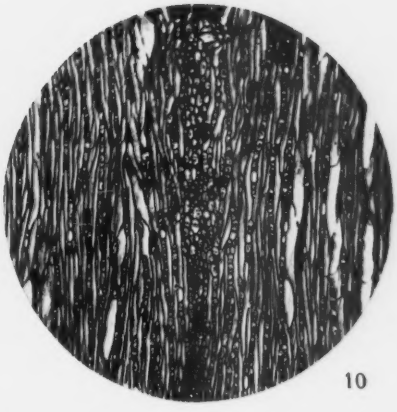

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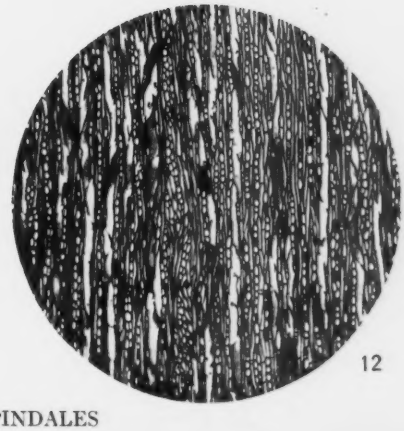


12

HOLDEN on SAPINDALES

THE MORPHOLOGY OF THE SEED OF BUCKWHEAT

NEIL E. STEVENS

(WITH EIGHT FIGURES)

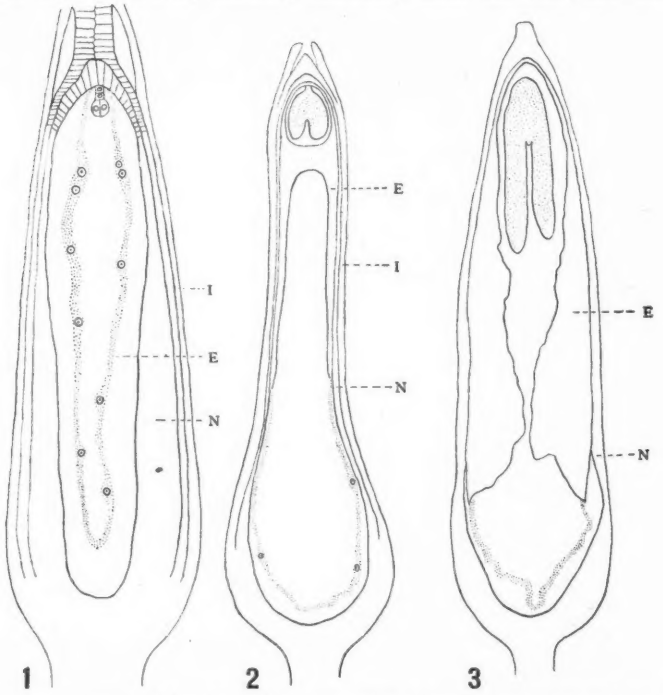
The Polygonaceae have been several times referred to in recent literature as being characterized by the production of seeds having an abundant perisperm (JOHNSON **7**, p. 337; COULTER and CHAMBERLAIN **3**, p. 179). This character has been taken by JOHNSON as an indication of rather close relationship between the Polygonaceae and the Piperaceae, in which family he has observed a perisperm. These statements as to the seed of the Polygonaceae are apparently based on the work of HARZ (**4**, p. 1072), who includes this family among the "Curvembryonaten," which he characterizes as "Eine grosse natürliche Gruppe . . . . alle ausgezeichnet durch den Besitz eines reichlichen mehlhaltigen Perisperms und eines meist peripherisch gelagerten Embryo." HARZ (p. 1102) figures and describes in considerable detail the structure of the buckwheat seed, and evidently considers the entire storage region as perisperm. He also states that the same condition occurs in species of *Rumex*. KRAEMER (**9**), to be sure, speaks of the Polygonaceae as having an endosperm, but does not discuss the morphology of the seed.

A careful study of the seed of *Fagopyrum esculentum* has convinced the writer that in this genus at least no perisperm is present at maturity. The material used in this study was collected during the summer of 1910 and fixed in Juel's fluid (JUEL **8**). Microtome sections were used exclusively. These were cut rather thick, usually about 12μ, and stained with Delafield's haematoxylin.

The early development of the embryo appears to be typical in every respect. In fact, up to the stage at which the cotyledons begin to be differentiated, the embryo corresponds almost cell for cell with the often figured *Capsella Bursa-pastoris*, in which, however, the suspensor is considerably longer.

Free nuclear division apparently begins in the embryo sac soon after fertilization, and by the time the embryo has reached the

quadrant stage (fig. 1), the endosperm contains at least 32 nuclei, held in the thin peripheral layer of cytoplasm. The nucellus at this stage is principally in the lower half of the ovulary cavity. A single layer, however, differing markedly from the rest, extends



FIGS. 1–3.—Fig. 1, longitudinal median section of ovule, showing the embryo in the quadrant stage and the endosperm in the free nuclear condition; the cells of the outer layer of the nucellus and the inner layer of the integument are outlined in the micropylar region; ×100; fig. 2, similar section about the time the cotyledons are first differentiated in the embryo; the upper portion of the endosperm has become cellular, while no cell walls have appeared in the lower portion; ×33; fig. 3, later stage, showing further development of the embryo and of the cellular portion of the endosperm; ×25; *I*, integuments; *N*, nucellus; *E*, endosperm.

to the micropyle. This outer layer becomes differentiated some time before fertilization, and consists of closely packed, regular cells, characterized by the possession of rather dense granular contents and the absence of a vacuole.

Growth and nuclear division are most rapid in the upper portion of the endosperm, that is, in the region between the growing embryo and the degenerating nucellar tissue. Cell formation begins in this region about the time the cotyledons first appear in the embryo. The cells arise centripetally and with great regularity. Apparently only a single nucleus is included in each cell, and there is no evidence of nuclear fusions. Cell formation gradually extends both above and below the region where it originates, and soon a marked differentiation is evident in the endosperm. At the stage shown in fig. 2, cell formation has progressed till a portion of the endosperm, some 8 or 10 cells thick, extends entirely across, just below the embryo. Above, around the developing embryo, the endosperm consists of only a single layer of cells; while below the thickest region, the endosperm becomes thinner, consisting toward the bottom of fewer and fewer layers of cells; till at the base, for at least a third of its length, the endosperm does not become divided into cells at all, but consists merely of a layer of cytoplasm with scattered nuclei, enclosing a large sap cavity.

This marked differentiation of the endosperm into two regions, one of which shows no cell formation whatever, suggested the chambered embryo sacs described by HOFMEISTER (**5**, p. 185), STRASBURGER (**11**, p. 111), and others, in which the first division of the primary endosperm nucleus is followed by the formation of a cross wall, dividing the embryo sac into two chambers, in only one of which the endosperm is developed. Careful study of early stages makes it seem certain, however, that no such cross wall occurs in the embryo sac of the buckwheat.

Soon after the stage just described, a secondary differentiation becomes evident in the cellular portion of the endosperm; the outer layer taking on the appearance and function of a cambium layer, which cuts off cells only on the inner side. A similar condition has been figured by CHAMBERLAIN (**2**, p. 344) in the developing endosperm of *Dioon edule*. These "cambium" cells divide rapidly; and the continued growth of the cells thus formed forces the wall of the ovary outward, and causes the more central portion of the endosperm to extend downward toward the base of the ovule. No further development occurs in the lower portion of the original

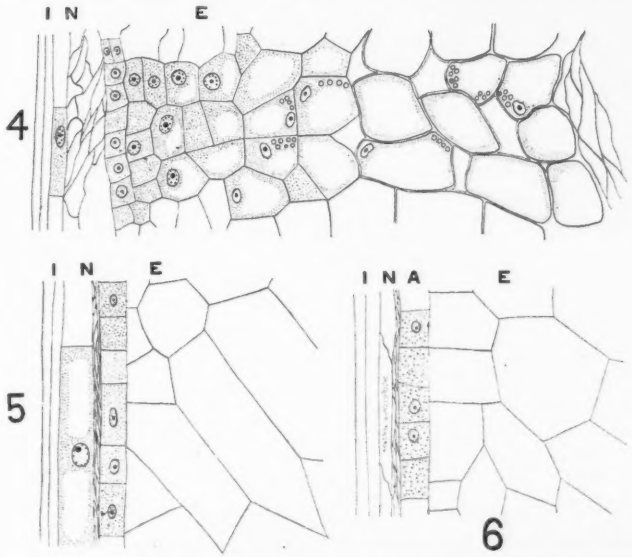
embryo sac (fig. 3). At the same time, the embryo is developing at the expense of the inner portion of the endosperm, so that the cells of the endosperm at this stage differ considerably in appearance. The "cambium" cells and the cells adjacent to them are thin-walled and closely packed. Nearer the center the cells become larger and vacuolate, some of them containing a considerable amount of starch; their walls also become slightly thicker, and the continued growth of the ovule pulls them apart, so that intercellular spaces of considerable size occur. Of the cells nearest the embryo only the crushed and distorted walls remain (fig. 4, *E*).

Nearly all the nucellar tissue has been destroyed by this time. The differentiated outer layer, however, persists in an actively growing condition, differing from the earlier stages only in that the cells have elongated and show, in some instances, small vacuoles (fig. 4, *N*). This outer layer of the nucellus is apparently composed of two quite different regions, which grade insensibly into each other. The upper portion, around the micropyle, consists of a plate of cells which apparently undergo no change after the time of fertilization. The cells of the lower portion continue to grow actively with very little if any cell division. They increase somewhat in thickness, and to a very marked degree in surface extent, keeping pace with the growth of the young seed. As the embryo nears maturity, these cells become more and more coarsely vacuolate (fig. 5, *N*), and in the mature seed only the crushed remains of this layer are present (fig. 6, *N*).

The fact that this layer persists in an actively growing condition till the growth of the endosperm is practically complete, together with the dense granular nature of the cell contents, suggests that it has a nutritive function, the "nutritive jacket" of COULTER and CHAMBERLAIN (**3**, p. 103). Similar layers, presumably nutritive in function, have been observed in numerous instances. Usually this "nutritive jacket" is derived from the integument; in one case however, *Armeria plantaginea*, BILLINGS (**1**, p. 278) describes such a layer, which he calls a "tapetum," as derived from the outer portion of the nucellus. In *Erodium gruinosum* BILLINGS finds this "tapetum" two layers thick, one layer of cells being derived from the integument and one from the nucellus. He describes a

"tapetum" derived from the integument in numerous genera, notably *Linum*, *Geranium*, *Primula*, *Phacelia*, and *Lobelia*.

LLOYD (**10**, p. 103) has recently shown that in the date the integument serves to some extent to distribute nutritive material to the developing endosperm. In the buckwheat, however, the integu-



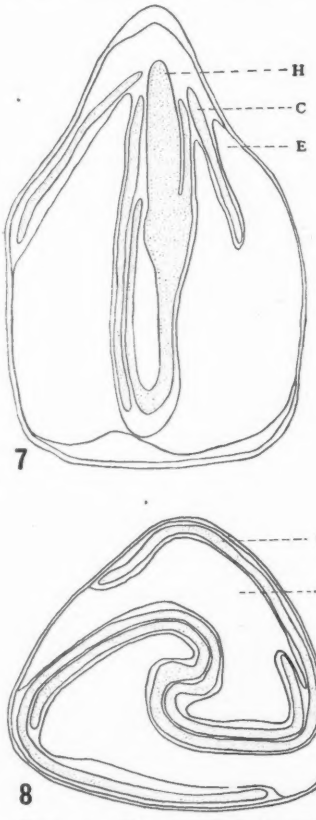
FIGS. 4–6.—Fig. 4, portion of longitudinal section at about the stage shown in fig. 3; only the outer layer of the nucellus, the "nutritive jacket," remains functional; the endosperm shows an outer layer of embryonic cells and a more central region of large vacuolate cells; some of the larger cells contain starch grains; ×260; fig. 5, later stage; the cells of the nutritive jacket have become vacuolate; ×260; fig. 6, mature grain; the nucellus remains merely as a thin region of crushed cells; the outer layer of endosperm cells is differentiated as an aleuron layer, the other endosperm cells are crowded with starch; ×260; *I*, integuments; *N*, nucellus; *E*, endosperm; *A*, aleuron layer.

ments seem to have no part in this process. In fact, they undergo very little differentiation, but remain throughout the growth of the seed as thin, rather uniform structures, each consisting of but two layers of cells. As there are no vessels present in the ovule which might accomplish this work, it seems entirely probable that the outer layer of the nucellus functions for the transfer of nutritive

substances from the chalazal region to the growing endosperm. Such an explanation might account for the fact that the endosperm develops fastest in the upper portion, the broken down cells of the nucellus forming, lower down, an effective barrier to the passage of food material.

In its later development the embryo becomes remarkably unsymmetrical, and as the cotyledons increase in size they become considerably curved. At maturity the cotyledons are broad and rather thin; and since the blade on one side of the midrib is twice as wide as on the other and the midribs lie together, one cotyledon on each side extends considerably beyond the other. In a cross section of the seed they present the appearance of a much exaggerated letter S (fig. 8, *C*). This peculiarly unsymmetrical nature of the embryo makes the endosperm exceedingly irregular.

Shortly before the seed is mature, a further differentiation takes place in the endosperm. The cambium layer, after it has ceased cutting off starch storing cells, divides further by anticlinal walls; thus forming a continuous layer of short regular cells, filled in the mature seed with dense granular contents, but containing no starch. This is an aleuron layer, the "eiweisshaltige Zellen" of HARZ (fig. 6, *A*). Except for this single aleuron layer, the irregular endosperm consists of large,



FIGS. 7, 8.—Fig. 7, longitudinal median section of mature seed; ×15; fig. 8, transverse section of mature seed, below the hypocotyl; ×15; the parts of the embryo are shaded; *E*, endosperm; *C*, cotyledons; *H*, hypocotyl.

closely packed cells, filled with starch. In its development the cellular portion has been crowded well down toward the base of the ovule. Even in the mature fruit, however, a space containing the remains of the undeveloped basal portion of the embryo sac is always present in the chalazal region (fig. 7).

The absence of a perisperm in the buckwheat does not of course exclude the possibility of its occurrence in other members of the Polygonaceae. That such a variation is sometimes found in nearly related genera is shown by the work of HUMPHREY (6) on the Scitaminales. In this order HUMPHREY found a progressive series of stages in the development of the endosperm. The Musaceae have a large starch bearing endosperm, in the Zingiberaceae and Cannaceae the endosperm is thin and contains only aleuron, while in the Marantaceae it is apparently not present in the mature seed. Variation occurs, as HUMPHREY shows, even within a single family. Among the Musaceae, *Heliconia* shows a distinct, though rather thin, starch bearing perisperm, while in *Strelitzia* only a thin layer of nucellar tissue showing no cellular structure remains in the mature seed. It is interesting to note that in the latter genus the massive endosperm never wholly fills the cavity of the seed, a condition comparable to that noted by the writer in *Fagopyrum*.

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BRIEFER ARTICLES

DEVELOPMENT OF THE ZYGOSPORE OF RHIZOPUS NIGRICANS

(PRELIMINARY NOTICE)

In growing *Rhizopus nigricans* for laboratory use, there was produced an unusual abundance of zygospores. This supply of material, and the increasing interest in the Mucorales in general, made it seem worth while to investigate the development of the zygospore of this species. Since completion of the investigation is temporarily delayed, the results so far obtained seem to be of sufficient interest to warrant the publication of a preliminary account.

There is a streaming of protoplasm with nuclei into the young suspensors, followed by a denser accumulation at the contact ends of the suspensors.

Before the gametangia are cut off, there appears a difference in the density and staining capacity of the protoplasm of the two suspensors, and this difference persists until the zygospore is mature.

The walls, cutting off the gametangia from each other, may not be formed simultaneously, and in each wall there is left a central pore. The wall which separates the gametangia from each other often thickens considerably before disintegration, and fragments of the thickened wall may be found in quite old zygospores. In the majority of zygospores the wall breaks down before any thickening occurs. In the late stages of the zygospore there is developed by the protoplast a thick, colorless, echinate coat, from which the brown coat may be removed, leaving the zygospore intact.

The many nuclei from each gametangium increase in size after the disintegration of the wall. All the nuclei except two disintegrate, and these two nuclei are imbedded in a coenocentrum. Preparations were submitted to Professor F. L. STEVENS, and he also identified this body as being like the coenocentrum of *Albugo*. There are indications that the coenocentrum has its origin at the point of contact of the two suspensors before the gametangia are cut off; but this needs further investigation. Neither fusion nor division of the nuclei has yet been observed. It is believed, however, that the two nuclei, left in the coenocentrum, fuse. From this stage to maturity many changes occur in the appearance of

the zygospore, but their interpretation is not yet clear. The coenocentrum persists until quite late, and in the mature zygospore there are many nuclei of the same size as those in the mycelium.

Oil is diffused throughout the young zygospore, but later the oil collects in larger globules. In the mature zygospore there is usually only one globule of oil in the center, and the protoplasm, unmixed with oil, is pressed in a comparatively thin layer against the wall.

These observations are based on the examination of over 2000 zygospores, sectioned serially, and much more material must be examined before the detailed account with illustrations will appear.—FLORENCE A. MCCORMICK, *The University of Chicago.*

A NEW CALIFORNIAN CEANOTHUS

Ceanothus fresnensis Dudley, sp. nov.—Low shrub, forming rounded mats, 2–4 dm. high, with stout rigid branches, young twigs tomentose: leaves opposite, oblanceolate to (and more commonly) broadly obovate, entire or usually irregularly denticulate toward the summit, coriaceous and involute, densely tomentose on both surfaces when young, glabrate above in age; petioles 1 mm. long, tomentose: umbels terminating very short branchlets; fruiting pedicels 8–12 mm. long: capsule 6 mm. high, about 5 mm. broad; horns subterminal, erect or spreading, 1 mm. long; styles very slender, divided to below the middle.

In foliage aspect this species closely resembles some forms of *Ceanothus vestitus*, but that is an erect shrub, often a meter high or more, with much smaller capsules, which are broader than long, and which have minute dorsal horns. In fruit characters it is closely akin to *Ceanothus cuneatus*, from which it differs primarily in its low habit and small tomentose, denticulate leaves.

The name, *Ceanothus fresnensis*, was proposed by the late Professor W. R. DUDLEY some ten years ago for a plant collected by HALL and CHANDLER in the southern Sierra Nevada. The label on the type specimen, which is deposited in the Dudley Herbarium of Stanford University, reads as follows: "Stevenson Mts., Pine Ridge, Fresno County, California, altitude 5300 feet, only locality seen. Growing with *C. cordulatus*." HALL and CHANDLER 407, June 1900. During the past summer I found another small colony about 100 miles north of the original station, at Confidence, Tuolumne County, where it was growing on a dry ridge at an altitude of 4000 feet in open yellow pine woods associated with *C. cordulatus* (ABRAMS 4727).—LEROY ABRAMS, *The Dudley Herbarium, Stanford University.*

CURRENT LITERATURE

BOOK REVIEWS

Heidenhain's "Plasma und Zelle"

The second part of HEIDENHAIN'S *Plasma und Zelle*[1] appeared early in 1911. While forming a part of BARDELEBEN'S *Handbuch der Anatomie des Menschen*, the section "Plasma und Zelle" is written from a remarkably broad standpoint, so that it is of general morphological and physiological interest.

In the first part,[2] issued four years ago, after a general discussion of the cell theory, the structure of the nucleus and of central bodies is taken up in detail, followed by an extensive critique of granular theories of protoplasm. Two leading tendencies give direction to the treatment of the subject matter: on the one hand, an attempt to break down the monopoly of the cell as the morphological and physiological unit; and on the other hand, more or less closely connected with this, an attempt to bring evidence for the existence of metamicroscopical units of structure, the *protomeres*. In this the author does not move in the realm of pure speculation, but is throughout concerned with arriving at conclusions establishing the existence and illuminating the nature of the metamicroscopical protomeres from a consideration of the organization and behavior of micro- and macroscopical structures. It is difficult to give in brief an adequate account of the materials and line of argument employed, and the reader is necessarily referred to the original.

The second part begins with a detailed treatment of the structure of the striated muscle, bringing together in a lucid fashion the mass of facts which has accumulated regarding this most complicated cytoplasm, doubly interesting because of the evident relation here between structure and function. A survey of this section again directs our attention to the meagerness of the data, a voluminous literature on the subject notwithstanding, regarding the histogenesis of the various structures of the muscle cell and its anomalous position with reference to information concerning the central body. It is the one conspicuous animal cell type in which even the mere presence of central bodies has not been demonstrated.

In discussing the relative solidity of various elements of the muscle cell, the author points out that the alternative *solid* or *liquid* does not put the question regarding the aggregate condition of cell constituents. He suggests

[1] HEIDENHAIN, M., Plasma und Zelle. Zweite Lief. pp. vi+604. Jena: Gustav Fischer. 1911.

[2] ———, Plasma und Zelle. Erste Abt. pp. viii+506. Jena: Gustav Fischer. 1907.

the conception of the *organized*, in which the elementary component particles maintain within certain limits definite relations to each other, although the structure as a whole may be highly plastic, as contrasted to the *fluid*.

It is to be regretted that the author did not feel warranted in giving a digest of the available data, such as they are, regarding the changes which take place in the structure of the striated muscle cell during contraction.

In connection with the discussion of the smooth muscle, the theory of short waves of contraction is developed. Whereas in the striated muscle the contraction wave has a length many times that of the muscle cell, in the smooth muscle it is but a fraction of the length of the cell. If contraction waves start simultaneously in all the fibrillae of a cell and keep step as they advance, the contraction knot of any fibrilla comes close to those of its neighbors, with a result that a more or less complete diaphragm is formed across the cell which, as it moves along, pushes the more liquid contents before it; a conception which HEIDENHAIN made use of in accounting for protoplasmic streaming in plant cells, and which has not been weakened by PFEFFER'S and RHUMBLER'S criticisms. The same conception is applied in a convincing manner to the movement of granules in pigment cells, and the suggestion is made that a similar situation obtains in dividing cells, resulting in the zonated appearance often observed in astrospheres. A further interesting application of the theory of short waves of contraction is made in discussing the contraction of cilia.

The section on the nervous substance brings together in an extensive but easily accessible manner the leading data on this highly complicated subject, which is of such importance to the cell theory. The author comes out unequivocally in favor of the neuron theory, a gratifying result for the adherents of this theory, especially since the standpoint of the author noted above would have made him keen to use any possible evidence against the cell theory. In the introduction a word is spoken for the importance of psychic processes as psychic processes in the economy of organisms and not as by-products of physico-chemical changes in the nerve substance. Considerable attention is given to the relation between nucleus and cytoplasm in the nerve cell. An interesting conclusion regarding the relation of the nucleus to regenerative processes in the protoplast results from the facts observed in the regeneration of a severed nerve fiber. Here, as in other known cases, repair proceeds from the nucleated portion of the cell, the other disintegrating. In the nerve fiber the cut surface may be a meter removed from the nucleus, so that a direct transportation of material from the nucleus to the region of injury is practically excluded, the action of the nucleus apparently being a dynamical one. The author also argues in favor of the "Tigroid" as a cytochromatin, an accessory chromatin developed in consequence of the huge cytoplasmic portion of the nerve cell.

A concluding chapter discusses the filar theories of protoplasmic structures and related matters.

The work contains an abundance of suggestions and information bearing

on the problems engaging the plant physiologist and morphologist. Mention should also be made of the wealth of excellent illustrations accompanying the text.—W. MARQUETTE.

The Eusporangiatae

CAMPBELL has published[3] a summary of the present knowledge concerning the morphology of the Ophioglossaceae and the Marattiaceae. His own studies of these forms have extended through twenty years, and his opportunities for observing and collecting tropical material have been unusual, so that such a summary is extremely valuable in bringing together the author's results and conclusions. The chief interest connected with this assemblage of plants is that in all probability it represents in the present flora the very ancient group which gave rise to seed plants. The main thesis of the work, however, is that Ophioglossaceae and Marattiaceae are genetically related, and that species of *Ophioglossum* are to be regarded as the most primitive forms of this assemblage, and in fact the most primitive living vascular plants. There is hardly room for difference of opinion today as to the close relationship that exists between the Ophioglossaceae and the Marattiaceae, and it is time to remove the Ophioglossaceae from their isolation as Ophioglossales, and to associate them with Marattiaceae as eusporangiate Filicales. As to the extremely primitive character of *Ophioglossum* and its relatively direct connection with the bryophytes, there is room for considerable difference of opinion.

The connection of *Ophioglossum* with bryophytes of the *Anthoceros* type is presented fully and skilfully. In embryogeny, the Eusporangiatae are characterized by the late development of the vegetative organs, as contrasted with the leptosporangiates, so that the young sporophyte is much more fully developed before it becomes independent of the gametophyte. In fact, several roots and leaves may be developed before independence, and in some cases even spores are formed before the two generations become completely separate. Moreover, the young sporophytes of *Ophioglossum* and *Anthoceros* resemble one another in appearance, with the massive foot in both cases, and the spore case of the latter represented by the cotyledon of the former. The author sees in this cotyledon, now sterile, a "pro-*Ophioglossum*" with a sporangiferous cotyledon, and with a stemless body, consisting of only leaf and root, the latter feature still being true of *O. moluccanum*. Of course the so-called "imbedded" sex organs of *Anthoceros* have long been recognized as a pteridophyte feature. The sperms of *Anthoceros* and *Ophioglossum* are regarded as perhaps the greatest obstacle, but if pteridophytes have been derived from bryophytes, that obstacle was overcome somewhere, either outside of the group or within it.

In reference to the subterranean gametophyte, which characterizes both

[3] CAMPBELL, D. H., The Eusporangiatae, the comparative morphology of the Ophioglossaceae and Marattiaceae. Carnegie Institution of Washington, Publ. no. 140. pp. vi+229. *pls. 13. figs. 192.* 1911.

Ophioglossum and *Lycopodium*, it is stated that there is "no question" that it is a secondary condition derived from such a gametophyte as that of *Marattia*, and probably through association with the symbiotic fungus. Of course it is known that the green, aerial portion of the gametophyte of certain species of *Lycopodium* is secondary, arising from the previously formed tuberous, subterranean portion, but it is conceivable that the gametophyte of *Ophioglossum* had a different origin. It is interesting to note in this connection, what may be of service to the author's view, that the gametophyte branches of some of the Anthocerotales become tuberous and subterranean, and that this habit is not unusual among liverworts.

In presenting the comparative morphology of Ophioglossaceae and Marattiaceae, the author has used the greatest variety of structures, but the conclusion as to genetic connection seems sound. In some cases the interpretations are at variance with what have come to be conventional; but, in the main, these unconventional interpretations have not so much to do with the relations of Ophioglossaceae and Marattiaceae as with the primitive character of the former among vascular plants. For example, to conclude that a short-necked archegonium is primitive as compared with a long-necked one, and that the collateral vascular strands of *Ophioglossum* are primitive and the concentric ones of the Marattiaceae replace them later, may be true for the reasons given, but it is unconventional. There seems to be no conception of the transition region as the one of vascular origins, and that the vascular systems of stem, root, and cotyledon are related to one another through it. However, since the transition region often appears to be merely a place rather than a definite structure, perhaps we have been laying too much stress upon it.

The general conclusion is that "from some form, allied to the simpler existing species of *Ophioglossum*, the whole fern series is descended"; that in this series "the leaf is the predominant organ, the stem at first being quite subordinate in importance"; that "this ancestral fern was monophyllous and the leaf at first was a sporophyll"; and that "from this central type presumably several lines diverged, of which only a few fragments exist." The details of structure and of lines of divergence are too numerous to cite; but the contribution as a whole is essential to every student of pteridophytes.—J. M. C

Cecidology

Probably the most important general work on cecidology recently published is KÜSTER'S *Die Gallen der Pflanzen*.[4] The author gives a clear and concise statement of the theories and problems which confront the botanist. In the preface he calls attention to the fact that there is no book on the general subject of gall formation, and that the recent literature has demonstrated the necessity of studying both the botanical and zoological phases of the subject. He also

[4] KÜSTER, ERNEST, Die Gallen der Pflanzen, ein lehrbuch für Botaniker und Entomologen. 8vo. pp. 437. *figs. 158*. Leipzig: S. Hirzel. 1911.

states that the work does not offer a solution of the perplexing problems or attempt a natural history study of the subject.

The introduction gives a brief résumé of the history of cecidology, of the research methods in use, and of the methods used in designating galls. Chap. i contains a brief discussion of the general groups of organisms which excite the formation of cecidia, including a list of the families and genera of insects, with the number of known European and Mediterranean species as given by HOWARD. The groups of plants which excite the formation of cecidia are given as follows: Myxomycetes, Bacteriaceae, Cyanophyaceae, Algae, Fungi, and Phanerogams. Examples are given for each group, but no complete lists of genera such as are given for the insects. Chap. ii gives a brief discussion of the host plants, showing that galls are to be found in all groups from lowest to highest, but are most abundant on the flowering plants. The chapter concludes with a list of the European and Mediterranean families of angiosperms, with the number of known galls (also according to HOWARD) on each. This list contains 109 families, the largest number of galls (901) being on Fagaceae. In this connection it is interesting to note that more than 4000 species of galls occur on 10 families of dicotyledons. Chap. iii (pp. 102) gives an excellent discussion of the morphology of galls. Chap. iv gives a good but not nearly so comprehensive a discussion of the anatomy of galls. Chap. v is a very brief discussion of the chemistry of galls.

Chap. vi is a most excellent discussion of the etiology of gall formation, and should be studied by all botanists and zoologists, especially by those who still believe that all insect galls are due to chemicals injected into the host plants by the mother insects. Attention is called to the lack of proof to substantiate the various theories, the obscure nature of the subject, and the failure thus far to produce artificially such galls as are formed by natural processes. Theories past and present, with arguments for each, are clearly stated, and the susceptibility of the host plant and its parts at various stages in its life history are given careful consideration. In this connection the author refers to facultative galls, or those in which the organism, although living within various parts of the host, can produce galls on certain parts only. In this chapter he states that in his opinion an understanding of gall building can be obtained only as a result of a comparative study of plant pathology. The chapter concludes with a discussion of the correlations between host plants and galls, of variations in galls, and of abnormal galls. Chap. vii, on the biology of galls, necessarily refers to a great deal of the discussion of the preceding chapters. After discussing the fact that some organisms attack and cause galls on many species of plants, the author takes up the relationship of the life-cycle of the parasite to the life-cycle of the host plant, the problem of biological species, gall ecology, distribution, paleontology, development and life of the gall, sexual dimorphism, opening of the galls and migration of the organisms, uses and injuries, resistance and immunity of the host plants, formation and action of poisons, inquilines, parasitic and saprophytic fungi

of galls. This chapter closes with a brief but interesting discussion of the galls formed on animals.

The work is a most comprehensive presentation of the modern aspects of the general subject of cecidology. The galls themselves are the subjects of primary consideration and the gall makers secondary. The entire subject is treated from the standpoint of the botanist, and galls are grouped with reference to their own characters and not the characters of their makers. Questions of taxonomy and alternation of generations are referred to only incidentally, but these subjects are well treated in other works on cecidology which are accessible to all energetic workers. The great bulk of the work is compiled from the writings of the Germans and French, who have been the most active investigators in this field. The author might well have given a little more attention, however, to the Italian, English, and American contributions. The work is timely and will find a welcome in every modern laboratory of general botany and plant pathology. In fact, it will be indispensable for those who expect to gain a broad and thorough knowledge of modern plant pathology.—MEL. T. COOK.

A plant physiology

In his *Plant physiology with special reference to plant production*, DUGGAR[5] has deviated far from the conventional type of texts on plant physiology. Of course the principles and even the facts of plant physiology are the same whether pure or applied. The main difference, therefore, is in the facts and principles emphasized. Unusual emphasis is laid upon mineral nutrients and soil problems, and upon factors of growth significant to crop production. A number of topics, not usually found in plant physiologies, are given a place: effect of weight and size of seed upon the vigor of the plants, parthenocarpic formation in pomaceous fruits, protection of crops by insecticides and fungicides, destruction of weeds by poison, etc.; while other phases of the subject, such as tropic, tactic, and nastic movements, are given little space. The author makes much use of material appearing in experiment station bulletins, a source little used in most texts.

No science is more fundamental to agriculture than plant physiology, and yet it has had little emphasis in the agricultural colleges and experiment stations of this country. It is certainly high time that this science takes its significant position in this field of production, and DUGGAR has given a start in the right direction. The book has the virtue of being concrete and teachable to beginners, and it is possible that the author has accomplished the double aim "to consider both the student and the general reader." Any teacher of beginners in the subject will appreciate the value of the concreteness in the text.

A careful perusal of the book leaves one feeling that it is more a selection

[5] DUGGAR, B. M., Plant physiology with special reference to plant production. Rural Science Series. 8vo. pp. xv+516. New York: Macmillan Co. 1911. $1.60.

and compilation of facts from the literature than a carefully digested product of it. It is in no sense critical and even lacks organization. This, of course, is in part a necessary outcome of the concreteness, and it is possible that it is the best sort of statement in view of the aim. Very seldom does the author refer to the fundamental physics and chemistry of plant activity. No mention is made of the application of the Van't Hoff temperature law of rate of chemical reaction or of the Weber-Fechner law to plant processes. Again, no adequate picture is given of the physics of the material and energy exchange of the foliage leaf, a set of processes which BROWN and ESCOMB have, in the main, reduced to pure physics. In this connection, we find the author emphasizing BLACKMAN'S misleading statement that the foliage leaf under illumination maintains a temperature considerably above the surrounding air. This is possible if the evaporation power of the air or the water supply of the leaf is low. On the other hand, if the water supply of the leaf and the evaporation power of the air are high, the leaf will maintain a temperature below that of the surrounding air whether illuminated or not. In spite of the fact that the significant work of BROWN and ESCOMB has been much cited, it has failed to have a sufficient influence upon the statements in texts.

The book is marked by carefully guarded statements, which is certainly a virtue in any scientific work; but this is often carried to an exasperating extreme, involving guards where our knowledge is sure. It is seldom that a text is so free from personal hobbies of the author.

The greatest disappointment in the book lies in the apparently careless way in which it was finished. Minor errors are numerous. Careful reading of a very few pages shows a number of these: p. 203, the use of the old term "cyanophyll" for the term chlorophyllin; p. 204, "aqueous carbon dioxide" for aqueous solution of carbonic acid; p. 205, "fruit sugar" for grape sugar. In many cases a change in phrasing or in choice of words would make the description much more telling; p 204, the author speaks of the decomposition of CO_2 and H_2O when the thing to be emphasized is the *reduction* of carbonic acid. The need of the criticism of the manuscript by a number of physiologists is evident.—WILLIAM CROCKER.

NOTES FOR STUDENTS

Current taxonomic literature.—J. C. ARTHUR (Bull. Torr. Bot. Club **38**: 369–378. 1911) in continuation of monographic work on the North American rusts records new species in *Puccinia* and *Uromyces*. A "Key to American and European *Allium* rusts" is included in the article.—H. H. BARTLETT (Rhodora **13**:163–165. 1911) has published a new species of *Euphorbia* (*E. arundelana*) from Maryland. The same author (*ibid.* 209–211. *pl. 93*) describes and illustrates a new species of *Oenothera* (*O. Tracyi*); the species is based on specimens grown from seed collected by S. M. TRACY near Tensaw, Ala.—W. H. BLANCHARD (*ibid.* 193–195) records a new variety of *Rubus* (*R. canadensis* var. *septemfoliolatus*) from Newfoundland; the same

author (*ibid.* 168–171) raises *Lycopodium complanatum* var. *flabelliforme* to specific rank, and (*ibid.* 55, 56) proposes a new name *Rubus amicalis* for *R. amabilis* Blanchard, not Focke.—T. S. BRANDEGEE (Univ. Calif. Pub. Botany **4**:177–194. 1911) in continuation of his work on Mexican plants has published 42 new species of flowering plants and describes a new genus (*Lithophytum*), doubtfully referred to the Solanaceae.—J. BRIQUET (Ann. Conserv. & Jard. Bot. Genève **13–14**:369–389 [29–49]. 1911) under the title "Decades plantarum novarum vel minus cognitarum" has published 11 new species of Caryophyllaceae and Labiatae from Mexico and South America.—N. L. BRITTON (Torreya **11**:130, 152. 1911) records two new species of *Opuntia*, *O. jamaicensis* from Jamaica and *O. Tracyi* from Mississippi. The same author (*ibid.* 174) describes a new *Hernandia* (*H. catalpifolia* Britt. & Harris) from Jamaica.—F. BUBÁK (Ber. Deutsch. Bot. Gesells. **29**:381–385. *pl. 14.* 1911) under the title "Ein neuer Pilz mit sympodialer Konidienbildung" describes and illustrates a new genus (*Acarosporium* Bubák & Vleugel) from Sweden. The fungus was found growing on dead leaves of *Betula odorata*.—R. E. BUCHANAN (Mycologia **3**:170–174. *pls. 50, 51.* 1911) in an article on the "Morphology of the genus *Cephalosporium*" describes and illustrates a new species and variety of this genus; both were obtained by isolation from humus-rich soil and grown on dextrose agar.—B. F. BUSH (Rhodora **13**:166–168. 1911) gives a synopsis of the Missouri species of *Rhexia*, recognizing three species, one (*R. latifolia*) being new to science.—J. CARDOT (Rev. Bryol. **38**:49–52. 1911) under the title "Deux genres nouveaux de la région magellanique" describes two new genera of mosses, namely *Neuroloma* and *Hygrodicranum*.—C. CHRISTENSEN (Rep. Nov. Sp. **9**:370–372. 1911) describes four new ferns, one (*Athyrium paucifrons*) being from Mexico.—F. S. COLLINS (Rhodora **13**:184–187. 1911) under the title "Notes on algae" describes a new species in the genus *Dermocarpa* from Barbados, and one in *Chantransia* from North Carolina; and to the latter genus several species are transferred from *Acrochaetium*.—E. B. COPELAND (Phil. Journ. Sci. Bot. **6**:65–92, 133–143, 145–148. *pls. 12–25.* 1911) has published some 65 new species of ferns from Borneo, the Philippine Islands, and Papua or New Guinea. Three new genera are proposed, namely: *Craspedodictyum*, *Dendroconche*, and *Merinthosorus*.—S. T. DUNN (Kew Bull. 310–313. 1911) describes a new genus (*Dipentodon*) from Yunnan, China; the genus is doubtfully placed in the Celastraceae.—W. W. EGGLESTON (Bull. Torr. Bot. Club **38**:243, 244. 1911) describes two new species of *Crataegus* from Massachusetts.—A. W. EVANS (*ibid.* 205–222. *pls. 9, 10*) records 34 species of Hepaticae from the Bahama Islands, of which two are new to science; and (*ibid.* 251–286. *pls. 11, 12*) in an article entitled "Hepaticae of Puerto Rico" proposes two new genera, namely, *Leptocolea*, based on *Lejeunea micrandroecia* Spruce, and *Aphanolejeunea*, based on *Jungermannia microscopica* Tayl. Several new species and new combinations are included in the article.—M. L. FERNALD (Rhodora **13**:109–162. *pls. 86–91.* 1911) gives a very interesting and significant account of a botanical expedition to Newfoundland and southern

Labrador during the summer of 1910. The author, after a careful study, concludes that "the indigenous flora of Newfoundland consists primarily of plants which occur to the north, in Labrador, or to the southwest, chiefly along the Atlantic seaboard or the Coastal Plain." Incidentally a new variety of *Carex* (*C. Hornschuchiana* Hoppe var. *laurentiana*) is recorded from Newfoundland and Anticosti.—M. L. FERNALD and K. M. WIEGAND (*ibid.* 188) record a new variety of *Epilobium* (*E. palustre* L. var. *longirameum*) from Labrador and Quebec.—F. W. FOXWORTHY (Phil. Journ. Sci. Bot. **6**:149–177. *pls. 26–33.* 1911) records 26 species of gymnosperms from the Philippine Islands, including a new species of *Podocarpus* and two hitherto unknown species of *Gnetum.*—T. C. FRYE (Proc. Wash. Acad. Sci. **12**:271–328. 1910) has published an illustrated taxonomic treatment of the "Polytrichaceae of western North America," recognizing for this region seven genera and about 26 species.—E. B. HARGER (Rhodora **13**:37–39. 1911) records a new species of *Arabis* (*A. viridis*) from New England.—H. HARMS (Rep. Nov. Sp. **9**:439, 440. 1911) has published a new species of *Poiretia* (*P. longipes*) from Brazil.—E. HEESE (Monats. für Kakteenk. **21**:132. 1911) describes and illustrates a new species of *Echinocactus* (*E. Gürkeanus*), introduced into European cultivation from Bolivia.—A. W. HILL (Kew Bull. 281–302. 1911) on "*Strychnos Ignatii* and other East Indian and Philippine species of *Strychnos*" recognizes about 24 species, some of which are new; a key to the species is included.—C. N. JENSEN and V. B. STEWART (Phytopathology **1**:120–125. 1911) in an article on "Anthracnose of *Schizanthus*" has published a new species of fungus (*Colletotrichum schizanthi*). The fungus was observed on various parts of *Schizanthus* at Ithaca, N.Y.—T. LOESENER (Rep. Nov. Sp. **9**:355–367. 1911) under the title "Mexikanische und zentralamerikanische Novitäten" has published several new species and varieties of flowering plants.—J. LUNELL (Am. Mid. Nat. **2**:122–128. 1911) records 4 new species and 8 new varieties of flowering plants from North Dakota and Minnesota.—A. H. MOORE (Bot. Jahrb. **45**:426, 427. 1911) gives a supplementary note on his recent monographic treatment of *Spilanthes*, recording further data on this genus, and includes descriptions of two new species from South America.—W. A. MURRILL (Mycologia **3**:165–169. *pl. 49.* 1911) under the heading "Illustrations of fungi IX" describes and illustrates several species, including a hitherto unrecorded species of *Hebeloma* (*H. praecox*) from New York; the same author (*ibid.* 189–199) in a third article on "The Agaricaceae of tropical North America" treats 6 genera, describing new species in *Clitocybe* (6), *Melanoleuca* (3), *Hydrocybe* (10), and *Hygrophorus* (2).—C. H. PECK (N.Y. State Mus. Bull. No. 150. pp. 100. *pls. 4, 6, 121–123.* 1911) presents the annual report of the state botanist for the year 1910, placing on record valuable data concerning particularly the flora of New York, and includes descriptions of 54 new species and varieties, mainly of fungi, but including also some flowering plants from different parts of the United States.—D. PRAIN (Kew Bull. 231, 232, 317, 318. 1911) has published 2 new genera (*Cyrtogonone* and *Discoglypremna*) of the

Euphorbiaceae from tropical Africa.—J. A. PURPUS (Monatsz. für Kakteenk. **21**:97–102. 1911) describes and illustrates a new species of *Mamillaria* (*M. valida*) from Mexico.—L. QUEHL (*ibid.* 119, 120. 1911) records a new species of *Echinocactus* (*E. nidulans*) from Mexico.—L. RADLKOFER (Phil. Journ. Sci. Bot. **6**:181–183. 1911) has published 4 new species of Sapindaceae from the Philippine Islands. The same author (Rep. Nov. Sp. **9**:372, 373. 1911) has described a new *Trichilia* (*T. stelligera*), and (*ibid.* 374–377) 5 new species in the Sapindaceae from Dutch Guiana.—C. B. ROBINSON (Phil. Journ. Sci. Bot. **6**:185–228. 1911) under the title "Botanical notes upon the Island of Polillo" gives a list of the plants known from this island and includes descriptions of 18 species new to science.—J. F. ROCK (Terr. Hawaii, Board Agr. & Forestry. Div. Forestry Bull. No. 1. pp. 1–14. *pls. 1–6.* 1911) records a new species of *Sapindus* and proposes a new genus (*Hibiscadelphus*) of the Malvaceae from the Hawaiian Islands.—R. A. ROLFE (Bot. Mag. t. 8392) has described and illustrated a new species of *Acineta* (*A. Moorei*) from South America.—E. ROSENSTOCK (Rep. Nov. Sp. **9**:342–344. 1911) has published 2 new species and a variety of ferns from Bolivia.—F. J. SEAVER (Mycologia **3**:207–230. *pls. 53, 54.* 1911) completes his consideration of "The Hypocreales of North America."—C. L. SHEAR (Phytopathology **1**:116–119. 1911) describes a new fungus (*Cryptosporella viticola*) which is said to be the cause of the so-called "dead-arm" of the grape.—P. A. SACCARDO (Ann. Mycol. **9**:249–257. 1911) under the title "Notae mycologicae" gives an annotated list of fungi, including descriptions of several new species, 4 of which are from New York and Florida.—V. SCHIFFNER (Oesterr. Bot. Zeitschr. **61**:261–264. 1911) in continuation of his studies on the genus *Metzgeria* records 2 new species from South America.—R. SCHLECHTER (Rep. Nov. Sp. **9**:428–439. 1911) has published several new species of orchids, including two from America and two from the Philippine Islands.—F. L. SCRIBNER (Bull. Torr. Bot. Club **38**:319–328. 1911) under the title "Notes on certain species of *Muhlenbergia*" records 2 new species in this genus from western United States and northern Mexico.—T. A. SPRAGUE (Bot. Mag. t. 8378. 1911) describes and illustrates a new species of *Columnea* (*C. gloriosa*) from Costa Rica. The plant has been introduced into cultivation at Erfurt, Germany, and at the Royal Botanic Gardens, Kew, England.—O. STAPF (Kew Bull. 318, 319. 1911) has published a new genus (*Sclerodactylon*) of the Gramineae from Madagascar.—F. STEPHANI (Hedwigia **51**:61–64. 1911) has proposed a new genus (*Goebeliella*) of Hepaticae, based on *Frullania cornigera* Mitt. The genus, as known at the present time, embraces two species, one from New Zealand, the other from New Caledonia.—G. SCWEINFURTH and R. MUSCHLER (Bot. Jarhb. **45**:428–430. 1911) propose a new genus (*Lifago*) of Compositae from Algiers.—H. and P. SYDOW (Ann. Mycol. **9**:142–146. *pl. 9.* 1911) under the title of "Novae fungorum species" have published several species new to science, including 4 from the Philippine Islands. The same authors (*ibid.* 277, 278) describe and figure a new generic type (*Scleropycnis*) which was found parasitic on branches

of *Abies excelsa* in the Erzgebirge.—I. URBAN (Bot. Jahrb. **45**:432–470. 1911) in co-operation with several specialists, under the title "Plantae novae andinae imprimis Weberbauerianae V," has published 72 new species of flowering plants from South America.—WOOD and FRANKS (Kew Bull. 274, 275. 1911) have published a new genus (*Siphonochilus*) of the Scitamineae from Natal.—H. F. WERNHAM (Journ. Bot. **49**:206–216. 1911) presents a revision of the American genus *Hamelia*, recognizing 27 species, of which one-third are characterized as new. The genus attains its greatest specific diversity in Mexico.—H. WOLFF (Rep. Nov. Sp. **9**:417–422. 1911) under the title "Umbelliferae Novae I" has published several new species and proposes the following new genera from Mexico: *Nematosciadium*, *Schiedeophytum*, and *Langlassea*.—N. WORONICHIN (Ann. Mycol. **9**:217–225. 1911) has characterized a new genus (*Physalosporina*) of the Pyrenomycetes. The genus, as at present understood, embraces 6 species having a distribution in the United States and Europe.—J. M. GREENMAN.

Biology of rusts.—The results of further studies on the biology of rusts are reported by FISCHER in two papers. The first one[6] is a continuation of a series of former studies, and includes four additional forms: *Uromyces caryophyllinus* (Schrank) Winter on *Saponaria ocymoides* L. and *Euphorbia Gerardiana* Jacq.; *Gymnosporangium tremelloides* Hartig on *Juniperus communis* L., *Sorbus Aria* (L.) Crantz, *S. chamaemespilus* (L.) Crantz, and the hybrid forms *S. hybrida* Koch (*S. aucuparia*×*S. Aria*) and *S. latifolia* (Lam.) Pers. (*S. Aria*×*S. torminalis*); *Ochrospora Sorbi* (Oud.) Diet. on *Aruncus sylvester* Kost. and *Anemone nemorosa* L.; and *Puccinia albulensis* P. Magn., a micro-*Puccinia* on *Veronica bellidioides* L. and *V. aphylla* L.

The discovery that the teleutospore generation belonging to *Aecidium Euphorbiae Gerardianae* occurs on members of the Caryophyllaceae serves as an illustration of the proposition formulated by FISCHER that on the hosts bearing the aecidial generation of certain heteroecious rusts there occur also micro- and lepto-forms whose teleutospores resemble the teleutospores of the heteroecious forms in question. The aecidium on *Euphorbia Gerardiana* has generally been regarded as belonging to *Uromyces excavatus* (DC.) P. Magnus on the same host; but the close resemblance between the teleutospores of *U. excavatus* and those of *U. caryophyllinus* occurring on members of the pink family led TRANZSCHEL to predict that the teleutospore form of *Aecidium Euphorbiae Gerardianae* would be found among the species of *Uromyces* parasitic on the Caryophyllaceae. The cultural work of FISCHER has shown the correctness of this prediction. It is probable that this resemblance, which has led to the discovery of the connection between aecidia and teleutospores in several cases, represents something more than a mere superficial similarity,

[6] FISCHER, ED., Beträge zur Entwicklungsgeschichte der Uredineen. Centralbl. Bakt. II. **28**:139–152. 1910.

and may be an indication of phylogenetic relationship between such heteroecious forms and the corresponding micro- and lepto-rusts. The cultural work with *Aecidium Euphorbiae Gerardianae* further showed that there exists a certain degree of specialization among the forms of *Uromyces caryophyllinus*, for of several members of the pink family *Saponaria* was the only one that could be infected by aecidiospores from *Euphorbia Gerardiana*.

Gymnosporangium tremelloides had therefore been experimentally connected only with the aecidium on *Sorbus Aria*, although *Aecidium penicillatum* Müller occurs on a large number of pomaceous plants. The present work adds to *Sorbus Aria* three new aecidial hosts, two of which are probably hybrids, with *S. Aria* as one parent. *Ochrospora Sorbi*, which occurs on various species of *Sorbus*, has been connected with *Aecidium leucospermum* by TRANZSCHEL, but the form on *Aruncus* (*Spiraea*) *sylvester* had not previously been connected with that aecidium.

In the second paper[7] the author's studies on the biology of the forms of *Gymnosporangium* are continued. He finds that the *Roestelia cornuta* on *Sorbus torminalis* (L.) Crantz and *S. latifolia* (Lam.) Pers. has its teleutospores on *Juniperus communis* L. The small cushion-like sori occur on the leaves and resemble those of *Gymnosporangium juniperinum* L. The new form is distinct from both *G. juniperinum* and *G. Amelanchieris*, however, as neither of these produce aecidia on *Sorbus torminalis* and *S. latifolia*. The author proposes the name *G. tormanili-juniperinum* for it.

Cultures with *Gymnosporangium juniperinum* extend the list of aecidial hosts of this species to include *Sorbus americana* DC. and *S. hybrida* Koch, in addition to *S. aucuparia* L., which was previously known. On account of the successful infection of *Sorbus americana*, the author suggests that this form is identical with the form occuring on *Juniperus Sibirica* Burgsd. (*J. nana* Willd.) in America, as the American form was shown by ARTHUR to have aecidia of the *cornuta*-type on *Sorbus americana*. The American form is called by ARTHUR *S. cornutum* (Pers.) Arthur.

Further cultures with teleutospores of *Gymnosporangium Amelanchieris* show that this form does not infect *Aronia nigra* Kochne, and is therefore not identical with *G. Davisii* Kern, which has aecidia of the *cornuta*-type on *Aronia nigra*. In conclusion, the author points out the fact that often hybrids of an immune and a susceptible species are susceptible. This condition, however, is not universally true.

TRANZSCHEL[8] reports the following results of cultures made in the years 1906 and 1907. *Puccinia Porri* (Sw.) Winter, sown on its host *Allium Schoenoprasum* L., produced uredinia and telia directly, without first forming spermagonia or aecidia. This rust, therefore, is a true hemi-*Puccinia*, and the

[7] FISCHER, ED., Studien zur Biologie von *Gymnosporangium juniperinum*. Zeitschr. Bot. **2**: 753–764. 1910.

[8] TRANZSCHEL, W., Beiträge zur Biologie der Uredineen. III. Travaux Musée Bot. Acad. Imp. Sci. St. Pétersbour **7**: 1–10. 1910.

existence of true hemi-forms is thus definitely demonstrated. *Aecidium Ligulariae* Thüm. on *Ligularia Sibirica* Cass. was connected with *Puccinia Eriophori* Thüm. on *Eriophorum angustifolium* Roth. *Senecio paluster* DC. was also shown to be an aecidial host for this form. *Puccinia litoralis* Rostr. was shown to have aecidia on *Sonchus oleraceus* L., *S. asper* Vill., and *S. arvensis* L. *Puccinia Dietrichiana*, described as new, on *Agropyrum caninum* P.B., was connected with *Aecidium Trolli* Blytt on *Trollius europaeus* L. Two forms on species of *Carex* were connected with aecidia on species of *Centaurea*. These are *Puccinia Jacea-leporinae* on *Carex leporina* L. and *Centaurea Jacea* L.; and *Puccinia Jacea-capillaris* on *Carex capillaris* L., *Centaurea Jacea* L., and *C. nigra* L. A third form on *Carex gynobasis* Vill. was found among aecidia-bearing plants of *Centaurea orientalis* L. These and other known forms, whose alternate hosts are species of *Carex* and *Centaurea*, the author proposes to unite under the collective name *Puccinia Centaureae-Caricis*. The different forms are closely restricted to their respective host species. *Lepidium Draba* L. and *Cleome spinosa* Jacq. were added to the known aecidial hosts of *Puccinia Isiacae* (Thüm.) Winter. Successful sowings of that species were also made on *Nasturtium palustre*, *Thlaspi arvense*, *Stellaria media*, *Galeopsis Tetrahit*, and *Raphanus sativus* L. *Puccinia Caricis* (Schum.) Rebout on *Carex pallescens* L. produced aecidia on *Urtica dioica* L. The same species on *Carex vaginata* Tausch. produced aecidia on *Urtica dioica* L. and *U. magellanica* Juss. *Carex pallescens*, *C. vaginata*, and *Urtica magellanica* are new hosts for *Puccinia caricis*. *Puccinia Maydis* Bering produced aecidia on *Oxalis stricta* L. and *O. cormiculata* L. *Pucincia Poarum* Nielson on *Poa nemoralis* L. var. *firmula* Gaud. produced aecidia on *Tussilago Farfara* L., but not on *Petasites officinalis* Moench. The aecidium on *Petasites officinalis*, therefore, which has been associated by several authors with *Puccinia Poarum*, does not belong to that rust. New cultures with *Uromyces Rumicis* Winter on *Rumex obtusifolius* again showed that this rust has its aecidium on *Ficaria*, which is also the aecidial host for other species of *Uromyces*. A form of *Uromyces Dactylidis* Otth. was successfully sown on *Ranunculus repens* L. and *R. bulbosus* L., on both of which aecidia were produced. A number of cultures of *Puccinia Veratri* Duby, *P. glumarum* (Schmidt) Erikss. and Henn., *P. Iridis* (DC.) Wallr., and *P. oblongata* (Link) Winter gave negative results.

In Japan, ORISHIMO[9] has shown that *Peridermium Pini-densiflorae* P. Henn., common there on the leaves of *Pinus densiflora*, belongs to the species of *Coleosporium* on *Aster scaber* Thunb. Six other species of *Aster* on which species of *Coleosporium* occur were not infected by aecidiospores of this *Peridermium*. The form is separated as *Coleosporium Pini-Asteris*.

For students of the Uredinales, attention should be called to FISCHER'S review[10] of work done on the biology of rusts in 1909.—H. HASSELBRING.

[9] ORISHIMO, Y., On the genetic connection between *Coleosporium* on *Aster scaber* and *Peridermium Pini-densiflorae* P. Henn. Bot. Mag. Tokyo **24**: 1–5. 1910.

[10] FISCHER, ED., Die Publication über die Biologie der Uredineen im Jahre 1909. Zeitschr. Bot. **2**: 332–337. 1910.

Spore formation among the Fungi imperfecti.—LEININGER[11] studying the factors affecting the reproduction of *Pestalozzia Palmarum*, finds that this fungus has four modes of spore formation, whose manifestation depends upon the conditions under which the fungus is growing. Spore formation can always be induced by withdrawal of nutriment; the mode of spore formation, however, depends largely on the nature of the medium in which the fungus is growing or has been grown previous to spore formation. On submersed mycelia or on mycelia which are submersed after having grown on other media, true pycnidia are formed. Mycelia which have grown in liquid media also produce pycnidia when placed in a damp atmosphere. Mycelia growing in air on the surface of liquids, or on solid substrata, produce pseudopycnidia, i.e., fruiting organs with a pseudo-parenchymatous base, but whose upper part is composed of a thin layer of interwoven hyphae. Sori, which are never covered, and solitary spores are produced only on liquid media. Some organic substances seem to favor the production of one or the other of the last two modes of reproduction. The author suggests that the polymorphism of such forms necessitates a reform in the classification of the *Fungi imperfecti* on a physiological basis.

Another paper dealing with the instability of definite modes of reproduction among the *Fungi imperfecti* is that by VOGES,[12] who makes the difference in the spore-producing structures of two forms of *Hendersonia* a basis for a discussion of the validity of the characteristics used in the classification of this group. The two species discussed are *H. piricola*, a leaf-inhabiting form on the leaves of pear trees, and *H. sarmentorum*, which occurs on the dead stems of many plants. In *H. piricola* the spores are formed in the epidermal cells and become exposed by the breaking of the cuticle. They are borne in sori, therefore, with no vestige of a perithecium. In *H. sarmentorum*, however, a well-developed perithecium is formed. These two forms, although related in other characteristics, would thus fall into entirely different orders of the *Fungi imperfecti*, and therefore the author regards the presence or absence of the perithecium as a characteristic of subordinate importance. The form of the spores and the number of cells they contain he likewise regards as of minor importance.

Such variations are known to occur very frequently among the *Fungi imperfecti*, particularly in cultures of the more complex forms. As the classification of this group is one of convenience and does not involve a taxonomic problem in the phylogenetic sense, it would be an error to lay great stress on such deviations which occur under special conditions or in a few forms, and to subordinate to them such conspicuous characteristics as the presence of a perithecium, which on the whole serve well for the distinctions of large groups of forms as they occur in nature.—H. HASSELBRING.

[11] LEININGER, H., Zur Morphologie und Physiologie der Fortpflanzung von *Pestalozzia Palmarum* Cooke. Centralb. Bakt. II. **29**:3–35. *figs. 15.* 1911.

[12] VOGES, E., Ueber die Pilzgattung *Hendersonia* Berk. Bot. Zeit. **68**:87–100. *figs. 10.* 1910.

Symbiosis of ants and plants.—RIDLEY,[13] as director of the botanic gardens at Singapore, has had exceptionally good opportunities to examine the so-called "myrmecophilous plants" of the eastern tropics, and he has reported his studies of more than a dozen such cases of symbiosis. His observations appear to have been carefully made and accurately recorded, and must be regarded as a considerable contribution to our knowledge of the relationship existing between these two organisms, even if we do not agree with all his interpretations of the facts.

A very considerable number of such plants afford a convenient sheltering home for the ants, either within hollow organs, such as thorns or stems, or within the leaves or flowers. The ants, however, obtain no food from the plant, nor do they benefit it in any way. Examples of this class are *Dischidia Rafflesiana* and several species of rattan. In *Goniothalmus Ridleyi* it seems likely that the ants effect pollination while nesting in and about its flowers.

In the second class of myrmecophilous plants, there seems to be a relationship which is mutually advantageous between many epiphytic ferns and orchids, whose roots afford an excellent shelter, and the insects that, in constructing their nests, bring up considerable quantities of soil and heap it about the base of the plants. To this class belong *Thamnopteris nidus-avis*, *Platycerium biforme*, and a considerable number of orchids.

A third class consists of two small trees, *Macaranga triloba* and *M. Griffithiana*, whose hollow stems are pierced and tenanted by ants. In both species the stipules are persistent and possess glands which secrete waxy granules that the ants gather and use as food. In return for this shelter and food, RIDLEY declares that the ants protect the trees from the attacks of caterpillars, although his only evidence seems to be that the trees tenanted by ants were not damaged by caterpillars, while certain others had their leaves somewhat eaten. He concludes that "the hollow stem, the retention of the stipules for some time after their original function of protecting the bud has ceased to be necessary, and the production of food bodies, are all modifications which can have no other function than that of attracting the ants and retaining their services as guards."—GEO. D. FULLER.

Movement of water in plants.—In a brilliant and ingenious piece of work on the movement of water in plants, RENNER[14] has brought some telling evidence for DIXON'S cohesion theory of the rise of sap. The evidence, too, is worked out by the use of that rather discredited instrument, the potometer. The cohesion theory, unlike the other conceptions of the rise of sap, has sound physics to recommend it, and now RENNER is able to measure suction in transpiring twigs amounting to 10–20 atmospheres, a thing that the cohesion theory assumes to exist. The "saturation deficit" is conceded by RENNER as the

[13] RIDLEY, H. M., Symbiosis of ants and plants. Ann. Botany **24**:457–483. 1910.

[14] RENNER, O., Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**:175–247. 1911.

cause of water movement. Whenever transpiration is occuring, a "saturation deficit" is produced in the cells of the region transpiring. This is the source of the "sucking power." When the loss of water is so great that the protoplast no longer exerts any pressure on the walls, the entire osmotic pressure of the cells is available for "sucking." The greatest suctions determined agree very closely with the osmotic pressures of the cells transpiring, as DIXON assumes to be the case. The method for getting the exact estimation of the greatest suction existing was ingenious. A twig that offered at one region great resistance to the movement of water (the resistance secured by tight clamping, double notching, or blocking of tracheae) was placed in a potometer. At a time when no "saturation deficit" existed, a determination was made of the rate of flow produced in the potometer by about 60 cm. of Hg. artificial suction. Through rapid transpiration the greatest "saturation deficit" was allowed to develop and the rate of flow it produced observed. The amount of suction involved in the second case could be figured from the known suction of the first, for it was found that the rate of flow was proportional to the suction. The maximum suction produced in forms like *Spirogyra* and *Helleborus* ranged from 10 to 20 atmospheres.—WILLIAM CROCKER.

Sand dunes of Illinois.—GLEASON'S[15] study of the vegetation of the sand deposits of Illinois is one of the most careful ecological surveys yet made of any region upon the continent. These deposits represent the most extensive areas with natural vegetation in the state, and cover over 8000 sq. km. The two most important types of vegetation are the grass lands, of which the bunch grass association, formerly covering nine-tenths of the entire sand area, is still conspicuous, and the forest, in which the black oak forms the typical association. This forest association, together with those composed of other species of oak which succeed it, are discussed elsewhere in some detail by HALL and INGALL[16], who give more emphasis to the economic than to the ecological aspect. It seems evident that the forest is slowly encroaching upon the prairie, although the advance of the oaks presents several unsolved problems. This tension line between forest and prairie is but one expression of the diverse elements of vegetation here in close contact, showing the unique position occupied by Illinois as a meeting ground for the great vegetational provinces of the north, south, east, and west.

Not only have the larger relationships existing between formations and associations received attention, but a careful analysis of the composition of each association is made, and the importance of the various constituent species estimated by the detailed study of many quadrants. An extensive list of these species is well annotated.—GEO. D. FULLER.

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[15] GLEASON, H. A., The vegetation of the inland sand deposits of Illinois. Bull. Ill. State Lab. Nat. Hist. **9**: 23–174. *pls. 1–20. figs. 6.* 1910.

[16] HALL, R. CLIFFORD, and INGALL, O. D., Forest conditions in Illinois. Bull. Ill. State Lab. Nat. Hist. **9**: 175–253. 1911.

Ecology of Australian algae.—The Yan Yean Reservoir, with an area of 1460 acres and an average depth of 24 feet, furnishes part of the water supply for the city of Melbourne, distant about 25 miles. From regular collections made from its waters for a period of 13 months, WEST[17] has studied the composition, distribution, and periodicity of its phytoplankton and its littoral algal flora. The most striking feature of the plankton is the richness of its desmid flora. The desmids reach their dominance during the warm period, from February to May, and their minimum during the succeeding cold months from June to October. During this cold period the crustaceans are dominant. The absence of the usual blue-green algal element at all times of the year is another noteworthy feature of the plankton.

The littoral algal flora is rich in species, contains many interesting types, and exhibits three rather well marked phases during the year. From November to January, with a rising temperature, there is a dominance of the Oedogoniaceae and Zygnemaceae, with an increasing quantity of the Desmidiaceae; these last reach their climax during the following warm months. The cold months of September and October show very little algal life. Of the 300 or more species of algae collected, 14 species and 11 varieties are described for the first time.—GEO. D. FULLER.

Vegetation of the Kermadec Islands.—From their position midway between New Zealand and the Polynesian Islands, these small islands of volcanic origin and subtropical climate exhibit many features of botanical interest. Sunday Island, the largest of the group, with an area of about 30 sq. km., has been visited by OLIVER,[18] who spent ten months studying the vegetation. An annual rainfall of about 225 cm., well distributed throughout the year, with the mild climate, produces a forest composed entirely of broad-leaved evergreens, with a conspicuous number of epiphytes. Among the tree members of this formation, two endemic tree ferns (*Cyathea*) are conspicuous, attaining a height of 20 m., and appearing as the dominant members of one of the forest associations. The epiphytes are principally filmy and other ferns. Only 12 of the 114 species of vascular plants are endemic, a small proportion when compared with the flora of other isolated Pacific islands, and this fact, along with certain geologic evidence, leads to the conclusion that the islands are not older than the Pliocene. The relationship of their flora with those of New Zealand, Australia, and Polynesia is traced.—GEO. D. FULLER.

Vegetation in the Dovrefjeld.—During a month spent in the upper Driva Valley, the WESTS[19] made an ecological survey of the alpine associations of

[17] WEST, G. S., The algae of the Yan Yean Reservoir, Victoria; a biological and ecological study. Jour. Linn. Soc. **39**:1–88. *pls. 6. figs. 10.* 1909.

[18] OLIVER, REGINALD B., Vegetation of the Kermadec Islands. Trans. New Zealand Inst. **42**:118–175. *pls. 18–33.* 1909.

[19] WEST, W. and G. S., Sketches of vegetation at home and abroad V. The ecology of the upper Driva Valley in the Dovrefjeld. New Phytol. **9**:353–374. *pls. 3, 4. figs. 23–32.* 1910.

the mountain slopes rising from partially cultivated rocky pastures near the river. A belt of woodland occupies the valley slopes up to an altitude of about 3600 feet, the montane forest consisting of *Betula odorata*, reaching a maximum height of 20 feet, with an undergrowth of *Betula nana*, *Juniperus nana*, *Empetrum nigrum*, and various species of *Salix* and *Vaccinium*, together with a rather abundant herbaceous vegetation. The shrubby members of this association persist in the belt of alpine shrubland, which reaches a poorly defined upper limit (4500–4800 ft.) with the disappearance of its most persistent members, *Salix reticulata* and *Betula nana*. Above is a luxuriant alpine lichen association, affording pasture for the reindeer and dotted with a variety of alpine flowers. Among the notes upon the many species examined, the scarcity of *Sphagnum* even in bogs is emphasized, and the results of a study of the variation at different altitudes of the leaves of *Betula nana*, both in size and structure, are recorded.—GEO. D. FULLER.

Parthenogenesis in Bennettites.—In 1894 LIGNIER published an account of the structure and affinities of *Bennettites Morieri*, and now, upon looking over his former preparations, he has come to the conclusion that the species was parthenogenetic.[20] The evidence is that the nucellar beak is not perforated or disorganized in any way, but is an absolutely continuous mass of primary tissue, that is, not tissue arising by proliferation and filling a passageway. The pollen chamber forms within the beak and extends more or less toward its tip, but never reaches the surface, so far as the author's preparations show. This is taken to prove that the observed embryos have developed in the absence of pollen tubes; it is recognized that they may or may not be parthenogenetic in the sense of arising from an unfertilized egg. It is further suggested that the parthenogenetic habit may have been the chief cause of the rapid disappearance of a group that was so flourishing during the Jurassic.—J. M. C.

Permeability.—CZAPEK[21] has brought together all his work on the effect of the surface tension of the surrounding fluid on the permeability of the Plasmahaut of the plant cell. Reviews[22] of preliminary articles have given the main points of this paper. Some evidence is offered that acids have their effect by interfering with the Plasmahaut emulsion. CZAPEK also doubts TRAUBE'S conception of osmosis, though his experiments offer little evidence against it. Many more substances were found which produced exosmosis of the cell contents of phanerogams only when their aqueous solutions had a surface tension of 0.68 (or less) of that of water. The Plasmahaut of

[20] LIGNIER, O., Le *Bennettites Morieri* (Sap. et Mar.) Lignier se reproduisait probablement par parthénogénèse. Bull. Soc. Bot. France **58**:224–227. 1911.

[21] CZAPEK, F., Ueber eine Methode zur Bestimmung der Oberflächenspannung der Plasmahaut von Pflanzenzellen. 8vo. pp. iv+86. *figs.* 3. Jena: Gustav Fischer. 1911. M. 2.60.

[22] BOT. GAZ. **50**:234. 1910, and **51**:472. 1911.

yeast apparently has a surface tension of about 0.60. The article seems to clear away much of the haze that has surrounded the matter of the significance of surface tension in cell activity.—WILLIAM CROCKER.

Underground organs of weeds.—Conflicting statements by various authors have induced PAMMEL and FOGEL[23] to investigate the organs of vegetative reproduction of some of our most common weeds. The Canada thistle (*Cirsium arvense*), the horse nettle (*Solanum carolinense*), the milkweed (*Asclepias syriaca*), and the bindweed (*Convolvulus arvensis*), were all found to be propagated by horizontal roots bearing adventitious buds; while in the wild morning glory (*Convolvulus Sepium*) and the quack grass (*Agropyron repens*), the organs of vegetative multiplication are rootstocks. In some instances the roots and subterranean stems resembled each other so closely that only by microscopic examination could the difference be detected.—GEO. D. FULLER.

Epidermis and light refraction.—FRIMMEL[24] thinks he has shown that the lower papillate epidermis of the leaves of the yew gives a total refraction of the light passing through the leaf from above, thereby leading to the use of all light that enters the leaf. He relates this character to the ability of the tree to grow in shaded habitats. He believes the lower epidermis of a number of other conifers acts in the same way. He finds a similar contrivance in the spongy parenchyma of the cotyledon of the beech. The fact of total refraction in the yew seems entirely established; whether it is of biological significance or not is quite another question.—WILLIAM CROCKER.

Arctic vegetation.—Hare Island off the coast of West Greenland, an uninhabited island 66 square miles in area, has been visited several times by PORSILD,[25] who has found a flora consisting of 82 arctic and 30 subarctic species. The vegetation belongs to the fell-field formation, large areas quite devoid of plants, passing into a poorly developed heath with arctic meadows and bogs in the more sheltered situations. Dispersal is almost entirely through the agency of the wind over the surface of the snow and frozen seas. The subarctic species are regarded as relics of milder climate in post-glacial times.—GEO. D. FULLER.

Pneumatophores.—From an examination of the tissues of vertical apogeotropic branches of the roots of *Terminalia Arjuna*, a large tree of Central India,

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[23] PAMMEL, L. H., and FOGEL, ESTELLE D., The underground organs of a few weeds. Proc. Iowa Acad. Sci. **16**:pp. 7. *pls. 5.* 1909.

[24] FRIMMEL, FRANZ V., Die untere Kutikula des *Taxus*-Blattes ein Lichtreflektor. Oester. Bot. Zeitsch. **61**:216–223. *figs. 4.* 1911.

[25] PORSILD, MORTEM P., The plant life of Hare Island off the coast of West Greenland. Saertryk af Meddelelser om Gronland **47**:252–274. *figs. 10.* Kobenhavn: Bianco Lunos. 1910.

ADAMSON[26] decides that they are developed "for purposes of aeration as shown by the great development of lacunar tissue." Both the horizontal and the vertical roots possess very loose cortical tissue with large lacunae, but most botanists would probably hesitate to pronounce upon the purpose of its development. The upright roots have well developed root caps, and possess no lenticels or other stem characters found in many pneumatophores.—GEO. D. FULLER.

Seed of Neuropteris.—In 1904 KIDSTON described the seed of *Neuropteris heterophylla*, which was said to be "as large as a hazelnut." Now the same investigator, associated with JONGMANS, has described[27] the seed of *N. obliqua* Brong., the specimens being in the Rijks Herbarium at Leyden. The seeds have the same general structure as those of *N. heterophylla*, but are about twice as large. This species of *Neuropteris* is also doubtless to be referred to the stem genus *Medullosa*.—J. M. C.

Root parasites.—MISS BENSON[28] has studied the structure of some haustoria on the roots of *Exocarpus* and *Thesium*, showing the nature of the penetration and connection with the roots of other plants. For a portion of the lignified elements of the haustoria the name "phloeotracheids" is suggested, and the investigator thinks they may act as a filter between the host and parasite, although the evidence that they have any such function does not seem to be at all convincing.—GEO. D. FULLER.

Calcium salts and fungi.—WEIR[29] concludes that soluble calcium salts are necessary to the complete development of higher fungi. *Coprinus plicatilis*, *C. papillatus*, *C. nivens*, and *C. ephemoides* showed little if any mycelial development, and no development of fruit heads or spores, when all the calcium present was in the form of the oxalate.—WILLIAM CROCKER.

A bog in central Illinois.—GATES[30] has instanced the meeting of northern and southern forms in a bog in central Illinois.—GEO. D. FULLER.

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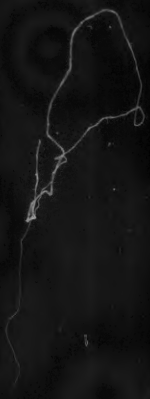
[26] ADAMSON, R. S., Note on the roots of *Terminalia Arjuna*. New Phytol. **9**: 150–156. *figs.* 3–7. 1910.

[27] KIDSTON, R., and JONGMANS, W. J., Sur la fructification de *Neuropteris obliqua* Bgt. Archiv. Néerl. Sci. III. B. **1**:25, 26. *pl.* 1. 1911.

[28] BENSON, MARGARET, Root parasitism in *Exocarpus* (with comparative notes on the haustoria of *Thesium*). Ann. Botany **24**:667–677. *pl.* 65. *figs.* 4. 1910.

[29] WEIR, JAMES R., Benötigt der Pilz *Coprinus* Kalksalze zu seinen physiologischen Funktionen. Flora **103**:87–90. 1911.

[30] GATES, F. C., A bog in central Illinois. Torreya **11**:205–211. 1911.



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